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Development of a Pollination Service Measurement (PSM) method using potted plant phytometry

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Abstract The value of pollination to human society is not limited to agricultural production, but also in the sustainability of ecosystems and the services that they provide. Seed set can be used as a comparative measure of pollination effectiveness, with minimum variability expected when other resources are not limiting. Six species of self-incompatible fall asters (*Symphyotrichum*) were used to evaluate pollination service at 12 sites across a spectrum of expected levels of pollination. Seed set per inflorescence was generally lower at sites with lower pollinator numbers and diversity, although as expected pollinator assemblage characteristics were highly variable within and between sites. However, rankings of sites showed consistency of response across phytometer species and between years; the summed ranks across multiple species appears to have as the greatest value in Pollination Service Measurement (PSM). Abundance, richness, and Shannon diversity of pollinator assemblages were highly autocorrelated and showed variable relationships with seed set depending on plant species and temporal scale of pollinator assemblage assessment. Use of seed set to directly measure pollination service at a site was consistent and cost effective when compared to less certain and more labour-intensive methods of pollinator collection and identification, and shows promise for implementation in pollination monitoring and bioassessment practices.

Keywords Sustainability · Ecosystem service · Pollinator conservation · Biomonitoring · *Symphyotrichum*

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Introduction

Conservation of native, wild pollinators is critical to ensuring the continued reproductive success and biodiversity of the plants on which ecosystem structure and function depend (Fontaine et al. 2006; Ollerton et al. 2011; Frund et al. 2013). Flowering plants form the trophic basis of productivity in most terrestrial ecosystems, and the maintenance and sustainability of plant populations, independent of human intervention, is crucial for the sustainability of the ecosystems themselves. Animal pollinators, including but not limited to bees, flies, butterflies, beetles, bats, and birds, play a vital role in mediating the sexual reproduction of approximately 85 % of the world's flowering plants, and 78 % in temperate regions such as southern Canada (Ollerton et al. 2011). While pollination in agricultural systems is routinely improved through the use of honey bees or other managed pollinators, similar approaches to pollination management in natural ecosystems are neither economically nor logistically feasible (Mader et al. 2010; Kjohl et al. 2011). Whether pollination service is

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delivered by wild or managed pollinators, or a combination thereof, there is a need for assessment and monitoring of pollination success in both agricultural and non-agricultural landscape elements.

Historically, bioassessment and biomonitoring methods have measured some aspect of community structure, such as richness, diversity, or abundance (Allan et al. 1997; Townsend et al. 1997; Woodcock et al. 2008; Liss et al. 2013), that acts as a proxy for ecosystem services or processes, or an (often poorly defined) concept of ecosystem "health" or "integrity." Using the community structure of organisms to infer the rate or quality of the ecosystem processes that they perform is common, but can have mixed or unpredictable results (Karr 1981; Callicott et al. 1999; Schwartz et al. 2000; Costanza 2012; Liss et al. 2013). High labour requirements for field sampling and sample processing, and the requirement for expensive taxonomic expertise, are significant drawbacks, and high variability in the resulting data makes interpretation difficult and development of appropriate responses difficult. In recent years, the development of approaches that directly measure ecosystem function has been encouraged, although none have been developed explicitly for pollination in a biomonitoring context. Evaluation of plant reproductive success using ambient vegetation or potted plant phytometers has been used to address a variety of ecological questions related to pollination. For example, seed set in crops or ambient vegetation has been used to examine landscape-level pollination service and competition among plants for pollinators (Greenleaf and Kremen 2006; Dauber et al. 2010; Trant et al. 2010; Hennig and Ghazoul 2011; Liss et al. 2013). Potted plants have been used to measure pollen limitation (Campbell 1985; McKinney and Goodell 2010), effects of neighbouring blooms on plant reproductive success (Kunin 1997; Bosch and Waser 2001; Schulke and Waser 2001; Spigler and Chang 2009; Lazaro and Totland 2010), and pollination responses to agricultural practices (Brittain et al. 2010a, b), and other habitat conditions (Steffan-Dewenter et al. 2002; Artz and Waddington 2006; Sperling and Lortie 2010).

The Pollination Service Measurement (PSM) system described here directly measures pollination service at a site by evaluating plant reproductive success (seed set) in a standard array of potted plants. This approach is expected to have the advantage of directly measuring the target ecosystem service rather than inferring it from pollinator assemblage data, and requires less time and technical expertise (and therefore incurs lower costs) than surveys of pollinator assemblages. For a plant to be useful as a phytometer for PSM, its seed set must indicate pollination by animal pollinators and no other means. The plant must therefore be non-apomictic (unable to set seed without pollination), an obligate outcrosser (dioecious or self-incompatible, unable to pollinate itself), and not wind-pollinated (its pollen must be transported exclusively by an animal vector). In addition, seed set must reflect levels of pollination limitation, rather than resource limitation or innate limits to numbers of seeds produced. For example, some species of *Asclepias* are reliant on insects for pollination but will produce very few seeds or fruit per inflorescence regardless of initial pollination success (Wyatt 1976; Neyland et al. 1999).

In this study, six species of fall asters (*Symphyotrichum*) which met the above requirements were used as the test species. Plants are grown in pots in a controlled environment with abundant, standard resources. Phytometers are experimental units of plants (single species or groups of several species) which are used to measure characteristics of an ecosystem in an area of interest for a variety of experimental purposes (Steffan-Dewenter et al. 2002; Albrecht et al. 2007; Sahli and Conner 2007; McKinney and Goodell 2010; Sperling and Lortie 2010). Phytometers also allow for replicability in both the environmental growing conditions and in the plant assemblage used to determine pollination success, allowing results obtained from different sites to be directly compared. This study will assess the utility of the PSM approach by examining seed set of the six *Symphyotrichum* species at multiple sites in southern Ontario, Canada. Multi-year sampling of pollinator assemblages (of varying intensity) at these sites indicates a broad gradient of abundance and diversity that allows evaluation of a priori expectations using PSM.

Materials and methods

Field sites

In 2011, test plants were deployed at five sites, at which pollinator sampling was ongoing as part of other studies. The sites covered a wide range of expected pollination service, based on the history of the sites and information gleaned from ongoing pollinator sampling (Table 1).

Table 1 Descriptions and expected pollination service (PS; based on long-term observations and/or sampling of the bee and syrphid assemblages) at the 12 study sites. Sampling and knowledge of the organic farm sites (CVF-1, 2) was insufficient to make a prediction of pollination service. All pollinator sampling occurred between May 1 and August 31

Site code	Site description and sampling history	No. of sampling events	Expected PS
EAS	Pollinator sampling via pan traps (4 blue and 4 yellow, 8 stations) and Malaise traps (3 stations) biweekly (2009, 2010) or monthly (2011)	28	Low
WAY	Pollinator sampling via pan traps (4 blue and 4 yellow, 8 stations) and Malaise traps (1 station) biweekly (2009, 2010) or monthly (2011)	28	Intermediate
BFE	Pollinator sampling via pan traps (blue and yellow, 8 stations) and Malaise traps (1 station) biweekly (2010, 2011) or monthly (2012)	21	Low
GSF	Pollinator sampling via pan traps (blue and yellow, 8 stations) and Malaise traps (1 station) biweekly (2010, 2011) or monthly (2012)	20	Intermediate
CCF	Pollinator sampling via pan traps (blue and yellow, 8 stations) and Malaise traps (1 station) biweekly (2010, 2011) or monthly (2012)	21	High
TSH	No sampling. Bee yard with >20 hives of honey bees	n/a	High
CVF-1	Organic farm, near front gate. Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at irregular intervals in 2011 and 2012	7	??
CVF-2	Organic farm, at forest margin next to production field (buckwheat). Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at irregular intervals in 2011 and 2012	7	??
LEN-A	Former soy field restored to tallgrass prairie community. Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at approximately monthly intervals in 2011 and 2012	6	High
LEN-N	Margin of fallow, unrestored field on same farm, for comparison. Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at approximately monthly intervals in 2011 and 2012	6	Intermediate
GIL-A	Hedgerow planted with wildflowers and including drilled nest sites in old stumps to encourage pollinators. Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at approximately monthly intervals in 2011 and 2012	6	High
GIL-N	Typical, unmodified hedgerow for the area, thick stand of white cedar (*Thuja occidentalis*) for comparison on same farm. Pollinator sampling via pan traps (4 blue and 4 yellow) and Malaise traps (1 station) at approximately monthly intervals in 2011 and 2012	6	Intermediate

Three sites were former agricultural (corn/soybean rotation) fields located at the Rare Charitable Research Reserve in Blair, Ontario. Pollinator data was available at each site for 2010–2012. Cruickston Creek Field (CCF; 43.377 N, 80.351 W) has been left to regenerate without human intervention since its final harvest in autumn 2003. Similarly, George Street Field (GSF; 43.377 N, 80.341 W) has been unmanaged since its final harvest in autumn 2006, and Blair Flats East (BFE; 43.385 N, 80.367 W) since autumn 2009. The decommissioned Eastview Landfill in Guelph, Ontario (EAS; 43.577 N, 80.232 W) was capped in the early 1990s and overseeded with a mix of grasses. Since that time, it has developed a community of plants dominated by non-native species. Monitoring from 2009 to 2011 indicated a low abundance of pollinators. Waynco (WAY; 43.328 N, 80.300 W) is a decommissioned gravel pit located south of Cambridge, Ontario. The site is intended for rehabilitation, but the current vegetation has regenerated without human intervention and has developed a community of plants dominated by non-native species. Monitoring at WAY from 2009 to 2011 indicated high abundance and diversity of wild pollinator species (occurrence of all species recovered listed in the Appendix).

In 2012, seven sites were added to the project. Townsend House (TSH) is the apiary and honey bee research centre at the University of Guelph (43.536 N, 80.214 W). Test plants were placed approximately 10 m from a group of approximately 20 honey bee hives, intended to represent the maximum achievable pollination in the field. Four sites were added at farm conservation projects supported by the Norfolk Alternative Land Use Services (ALUS). This is a successful program in Norfolk County, Ontario "providing payments to farmers for returning marginal, environmentally

sensitive, or inefficient farmland into native vegetative cover and wetlands" (www.norfolkalus.com). Two pairs of sites (with pollinator monitoring data from 2011 and 2012) were selected. Each pair consists of a conservation project site and a comparable nearby unamended site. GIL sites include a hedgerow project modified for pollinator conservation (GIL-A; planted wildflowers, blooming shrubs, holes drilled for cavity-nesting bees) and an unmodified cedar (*Thuja occidentalis*) hedgerow typical of the area (GIL-N). LEN sites consist of a prairie restored from field crop use, specifically intended to support native insects for pollination of a high-value fruit crop (LEN-A), and a grassy, unmodified area at the margin of a soybean field on the other side of the property (LEN-N). Per conditions of our permission to conduct research at ALUS sites, exact locations and names of individual property owners are not included. Cherryvale Farm (CVF) was a large organic and permaculture farm located in Cherry Valley, Prince Edward County, Ontario (43.933 N, 77.147 W). Test plants were placed on the farm at two locations (CVF-1, CVF-2) corresponding with pollinator monitoring sites from 2011 and 2012.

Pollinator sampling

Two major groups of pollinators (bees, syrphid flies) form the basis of the pollinator assemblage descriptors for these sites. No pollinators were collected at TSH, where the assemblage was expected to be dominated by *Apis mellifera*. Sampling equipment was deployed for 48 h at 2–4-week intervals depending on the site, in good flying weather for pollinators whenever possible. All sampled sites had one Malaise trap, with the exception of EAS with three. Sites had varying numbers of permanent sample plots containing yellow and blue pan traps. To correct for variable sampling approaches and intensity, a "standard unit" (SU) consisting of [eight blue plus eight yellow pan traps] plus one Malaise trap per sampling date is used. Specimens were identified to genus and distributed to taxonomists for species-level identification to species where possible. Total richness was also estimated using extrapolation of the rarefaction curve (EstimateS version 9.1.0, Colwell 2013).

Test plants and seed set

All test plants were obtained in 72-plug trays from St. Williams Nursery and Ecology Center in Walsingham, Ontario (www.stwilliamsnursery.com). This source was chosen because seed is collected from wild populations, and thus it is not expected to have issues of self-incompatibility that may be associated with nursery stock where seeds may be collected from only a few parents. Seed collected from wild populations can reasonably be expected to have similar relatedness levels as the source populations. In 2011, three species of *Symphyotrichum* (*Symphyotrichum puniceum*, *Symphyotrichum ericoides*, *Symphyotrichum cordifolium*) were deployed at the original five sites. In 2012, these three species, plus *Symphyotrichum oolentangiensis*, *Symphyotrichum pilosum*, and *Symphyotrichum novae-angliae* were deployed at the expanded list of 12 sites, except *S. cordifolium* and *S. novae-angliae* were not deployed at CVF sites due to limited availability of specimens (Table 2).

Plants were transplanted from the plug trays to individual 15 cm plastic pots, using a standard potting mix for all species. The plants were watered twice weekly with untreated well water. Six plants of each species were randomly assigned to each of the study sites. When flower buds formed, two branches were haphazardly selected on each plant, one as an open-pollinated branch that would be exposed to flower visitors in the field (TRT), the other as a control (CON). Plants remained in the greenhouse until just before flowering, at which time any open blooms on the TRT and CON stems were removed and the test branches on each plant were bagged with mesh pollinator exclusion bags (PEBs). Plants were watered well and placed in a group at a point near the middle of the site in full sun, and PEBs were removed from the treatment (TRT) stems only. Grouping of the plants is necessary to ensure that there is a source of pollen in habitats where wild individuals do not occur, which was usually the case. After 7 days (more for some species at CVF), the TRT stems were re-bagged, plants were returned to the greenhouse, and the regular watering schedule resumed. PEBs remained in place until seeds were set. Flower heads were harvested and returned to the laboratory where filled seeds were enumerated using a dissecting microscope (Fig. 1).

Statistical analysis

Pollinator abundance, taxa richness, and Shannon–Wiener diversity (H') per SU were compared between sites using one-way analyses of variance (ANOVA) with trap catches

Table 2 Summary of deployment dates for all fall aster species at the study sites. "–" indicates that species was not deployed at that site in that year, "X" indicates that the plants died at that site, most frequently due to summer drought conditions, although *S. ericoides* died for unknown reasons at three sites. Other losses were related to predation (groundhog and/or white-tailed deer)

Site	New England (*S. novae-angliae*)	Sky-blue (*S. oolentangiensis*)	Purplestem (*S. puniceum*)	Heath (*S. ericoides*)	Hairy (*S. pilosum*)	Heart-leaf (*S. cordifolium*)
2011						
EAS	–	–	9/23–30	9/30–10/7	–	10/6–10/13
WAY	–	–	9/23–30	9/30–10/7	–	10/6–10/13
BFE	–	–	9/23–30	9/30–10/7	–	10/6–10/13
GSF	–	–	X	9/30–10/7	–	10/6–10/13
CCF	–	–	9/23–30	9/30–10/7	–	10/6–10/13
2012						
EAS	9/11–18	9/11–18	9/18–25	9/18–25	9/25–10/2	9/25–10/2
WAY	9/11–18	9/11–18	9/18–25	9/18–25	9/25–10/2	9/25–10/2
BFE	9/11–18	9/11–18	9/18–25	X	9/25–10/2	9/25–10/2
GSF	9/11–18	9/11–18	9/18–25	X	9/25–10/2	9/25–10/2
CCF	9/11–18	9/11–18	9/18–25	9/18–25	9/25–10/2	9/25–10/2
TSH	9/11–18	9/11–18	9/18–25	9/18–25	9/25–10/2	9/25–10/2
CVF-1	–	9/11–18	9/18–28	9/18–28	9/18–28	–
CVF-2	–	9/11–18	9/18–28	X	9/18–28	–
LEN-N	9/12–19	9/12–19	9/19–26	9/19–26	9/26–10/3	9/26–10/3
LEN-A	9/12–19	9/12–19	9/19–26	9/19–26	9/26–10/3	9/26–10/3
GIL-N	9/12–19	9/12–19	9/19–26	9/19–26	9/26–10/3	9/26–10/3
GIL-A	9/12–19	9/12–19	9/19–26	9/19–26	9/26–10/3	9/26–10/3

per SU on each date serving as replicates. Mean assemblage values were calculated for all available samples between 2010 and 2012, depending on the site. Year 2012 insect samples were not available for EAS or WAY. Differences between sites were determined using a Tukey post hoc test (α=0.05).

Seed set data were analysed separately for 2011 and 2012 due to the different numbers of species and study

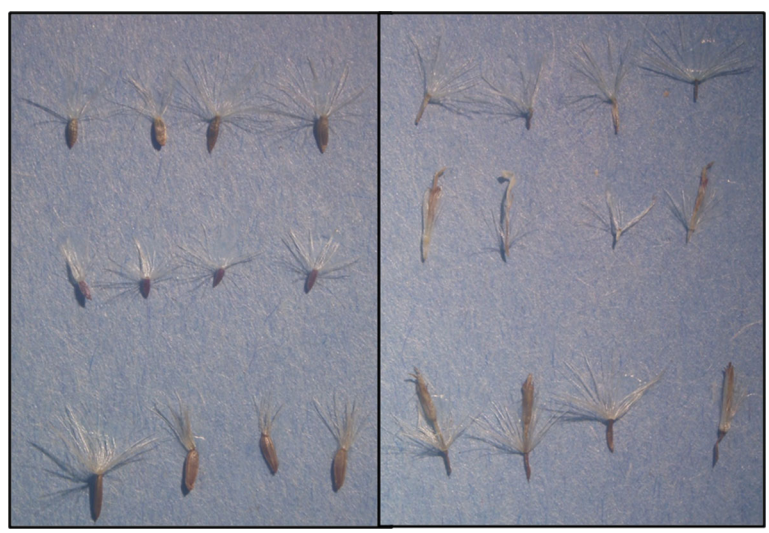

Fig. 1 Examples of fertilized (L) and unfertilized (R) seeds from three of the *Symphyotrichum* species used in the experiments (*top*—*S. cordifolium*; *middle*—*S. ericoides*; *bottom*—*S. puniceum*)

sites. The self-incompatibility of each species was confirmed using a paired *t* test comparing seeds per flower on TRT vs. CON branches. An ANOVA of seed set on TRT branches for each test species was conducted to assess differences between sites, using the mean number of seeds per flower on each of the experimental plants. Thus, each plant is an experimental unit (not each flower), and $n=6$ at each site. For those plants that were deployed for 11 days at Cherryvale Farm in 2012 (Table 2), seeds per flower was multiplied by [7/(# days deployed)] to standardize deployment time to 1 week. Differences between sites were assessed using a Tukey post hoc test ($\alpha=0.05$). Seed set across all species and all sites was analysed within years using a non-parametric ANOVA (Kruskal–Wallis) of site ranks, with missing data points replaced by the mean of the other ranks for the site.

Results

Insect assemblages

A list of bee and syrphid taxa recovered at each site by pan and Malaise traps is provided in the Appendix. Due to large differences in sampling effort at the sites, total richness is not directly comparable (Table 1), and some sites have considerable undocumented richness. In 2012, ANOVAs were performed using all available samples, since this most closely represents the season-long pollination service that was the target for evaluation. All three assemblage metrics (n, R, H') showed high variance, but statistically significant differences were detected among the sites in richness ($p<0.001$) and H' ($p<0.002$). Differences in pollinator abundance were not statistically significant, although mean abundance per sampling event varied threefold. Abundance, richness, and H' were highly correlated, as in 2011. On a per-sample basis, richness was significantly greater at WAY than CVF-1 or GIL-A, and H' was greater at CVF-2 and CCF than at GIL-A. No other differences were statistically significant among these descriptors. As expected, extrapolation of rarefaction curves indicated that season-long richness estimates at intensively sampled sites (BFE, CCF, GSF, EAS, WAY) were superior to those at the remaining sites, and were not well-correlated with PSM (see Appendix). Sites with only six or seven sampling events had highly suspect extrapolations that seem likely to underestimate total richness.

Seed set

The lack of statistically significant seed set in the CON plants of all species and during both years indicates that they were self-incompatible and therefore were suitable choices as phytometers for PSM. Several problems arose during the experiment that resulted in loss of plants and a consequent loss of replication in the analysis. One source of loss was herbivory, possibly by white-tailed deer or groundhog, which was particularly a problem for *S. puniceum*. This resulted in the loss of all *S. puniceum* at GSF in 2011, and a few individual plants elsewhere. The second was the delayed bloom of *S. cordifolium* in 2011, which resulted in many flowers not being receptive while in the field, although deployment was delayed as long as possible. Wild specimens were observed to bloom in September, but the buds of greenhouse-grown specimens did not open, and it seems that light from an adjacent greenhouse was preventing bloom in this short-day plant, reducing sample size considerably in 2011. In 2012, plants were raised in a greenhouse that receives ambient light only and issues with delayed bloom were not detected. A few specimens of *S. ericoides* were lost to an apparent disease that killed the flowers on some branches.

In 2011, no significant differences in TRT seed set between sites were observed (Fig. 2). For plant species and sites tested in both years, seed set per inflorescence was similar between years. ANOVA of seeds per inflorescence on the TRT branches for each species revealed no statistically significant differences between sites for *S. oolentangiensis*, *S. puniceum*, or *S. pilosum*. The remaining three species did have differences between the highest and lowest seed set values (Fig. 3). A wide range of responses were observed, and sites ranked by seed set were similar across the species (Table 3). The non-parametric (Kruskal–Wallis) ANOVA of ranked seed set by site showed no significant difference in 2011 ($n=3$), but there were significant differences among sites in 2012 ($n=6$, $p<0.001$; Fig. 4). When all species were ranked according to seed set per inflorescence, the sites with the highest seed set were generally the Norfolk County conservation study sites (both experimental and control) and CCF, the oldest of the old-field sites. CVF-1, EAS, TSH, and WAY were lowest. The results at WAY were unexpected, since seed set and the pollinator assemblage were strong there in 2011. However, as the site is an abandoned gravel pit with poor and dry soil, the drought of summer 2012 may

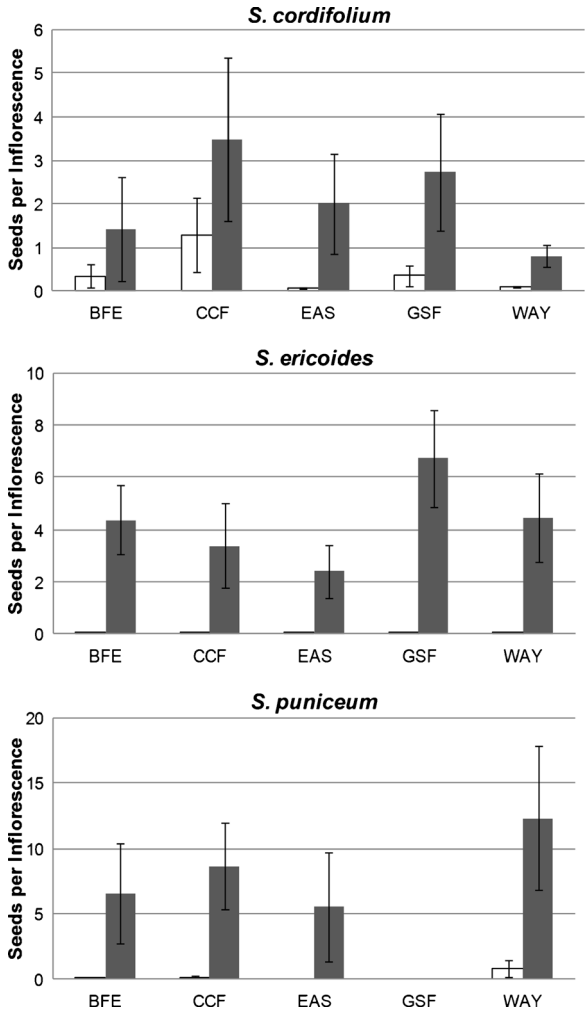

Fig. 2 Mean seed set per inflorescence of the study plants (*white*—control; *black*—open-pollinated) for the five study sites used in 2011. *Error bars* indicated 1 S.E

have negatively impacted pollinators more strongly in comparison to other sites. The low seed set at TSH suggests that honey bees did not forage extensively on *Symphyotrichum* flowers, which was unexpected, and activity of other pollinators in proximity to numerous honey bee hives may have been diminished.

Discussion

A wide range of the response variable (seeds per inflorescence) was possible for all plant species, both in terms of the number of florets per inflorescence and the presence of multiple inflorescences per branch. Typical of the Asteraceae, the florets at the outer edge of each individual inflorescence become receptive first. Florets undergo anthesis, and pollen is pushed to the top of the floret by the (as yet unreceptive) pistil. A day or two later, the stigmatic lobes open to expose the receptive surface. This proceeds inwards in concentric rings until the central disc florets bloom several days after the ray florets. Full pollination of an inflorescence would therefore require multiple visits by pollinators over the period of bloom. The number of florets, and hence the number of potential seeds per flower, vary among the species from *S. ericoides* with about 20 ovules per inflorescence, to *S. novae-angliae* with 150 or more per inflorescence (Chmielewski and Semple 2003). Therefore, even the sites exhibiting the highest seed set were only about 60 % of this theoretical maximum. Due to the constraints of time, however, pollen limitation experiments could not be conducted to determine the actual maximum seed set of the experimental species.

Some notable exceptions notwithstanding, the overall results of the experiments showed consistency with a priori expectations in both years, based on observations of the pollinator assemblages present at the study sites during monitoring over several years (Table 1). In 2011, EAS and BFE were expected a priori to have the lowest seed sets, and ranked no higher than third for any of the plant species tested (Table 3). EAS, expected to be the lowest, did rank lowest for two species. In 2012, the ranking of all sites was generally as expected. All of the sites used in 2011 ranked lower than most of the new sites, although absolute seed set was generally comparable within sites between the 2 years (Figs. 2 and 3). The similar ranking of sites between years indicates the success of the approach. Unexpected results were seen at WAY (low seed set, possibly related to the locally arid conditions) and at TSH, where honey bees did not effectively pollinate the test plants. Using only those species and sites examined in both years, the ranking of sites by PSM was similar: (for 2011: EAS < BFE < WAY < CCF < GSF, for 2012: EAS=BFE < WAY < GSF < CCF) indicating PSM is generally consistent across years and across species, and gives a relative (if not absolute) estimate of PSM at a site when compared to other sites. Most notably, the ALUS sites that were undergoing conservation projects ranked higher than their control sites, despite the projects being less than 5 years old and in close proximity to the controls.

It should be noted that the complexity of PSM analysis was considerably less than would have been the

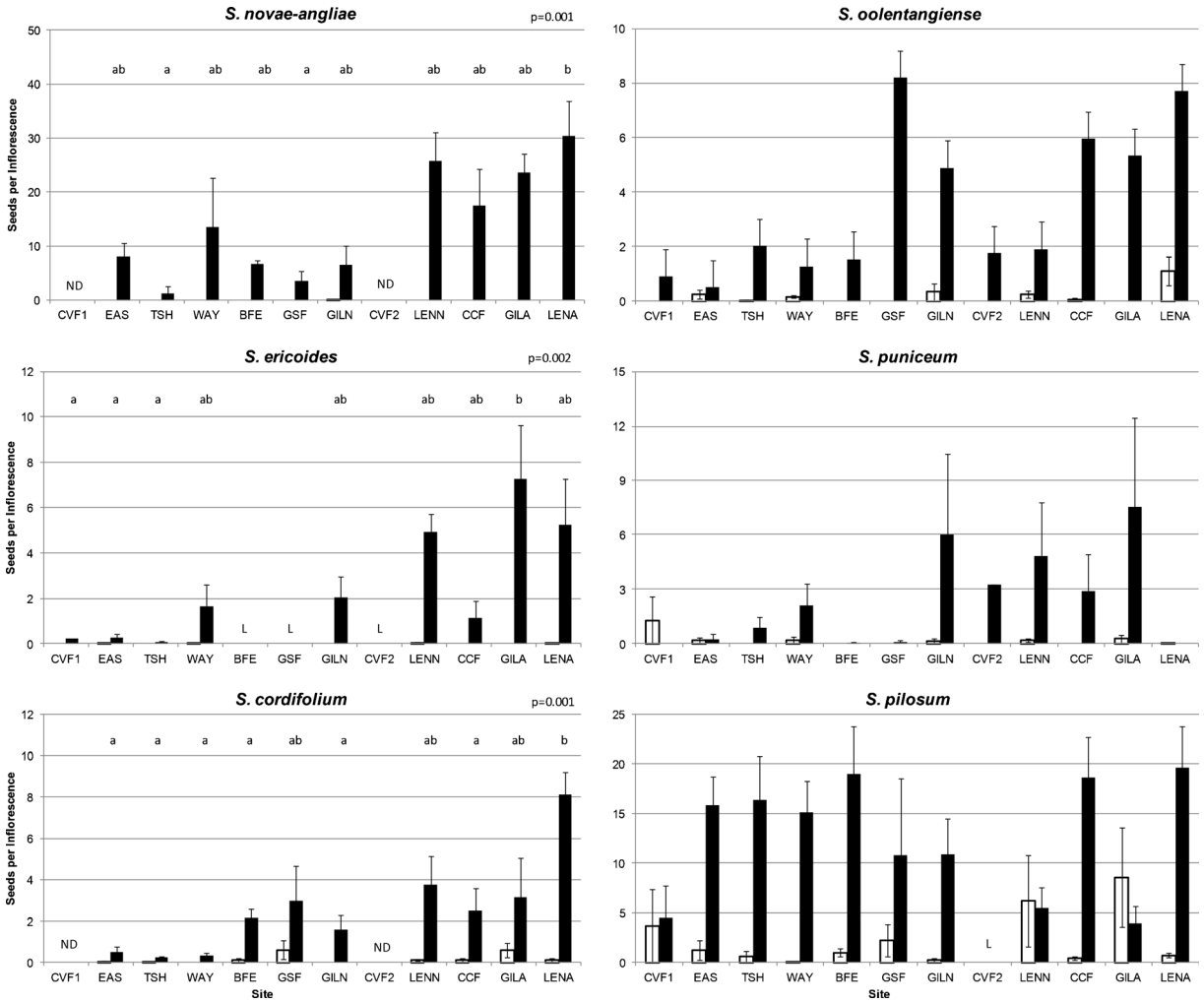

Fig. 3 Seed set of six species of *Symphyotrichum* at the study sites in 2012 (control=*white bars*, treatment=*black bars*). *ND* indicates that plant species were not deployed at that site, *L* indicates those lost in the field due to herbivory or other mortality. *Bars sharing the same letter code* are not significantly different from one another (GLM, Tukey test, α=0.05). *Error bars* show 1 S.E

case for pollinator assemblage sampling, and differences in assemblage between sites would be likely no easier to detect, nor could differences in assemblage be simply linked to differences in pollination. This method does not require specialized knowledge or skill to execute, and fruits containing filled seeds for all species are easily distinguished from those that are unfertilized (Fig. 1). Herbivory was a minor mortality source in the field. However, in the future, an increase in sample size to eight or even ten plants per site may be warranted, possibly divided into two groups a standard distance apart (e.g. 20 or 50 m). Additional plant species that sample different times of year or the activity of particular pollinators or groups of pollinators should be evaluated for use. Ultimately, a more complete system could be developed, using an array of plants suitable to an area and measuring seasonal PSM and also segments of the pollinator assemblage or times of year that are of particular interest (for example, pollination provided by bumble bees or other groups of concern, spring pollination service). This PSM system shows promise for evaluating pollination success directly, rather than inferring it from pollinator collections. It is less costly in money, labour, and expertise than systems that rely on pollinator community sampling.

The goal of this study was to compare and monitor pollination service, rather than to make statements about the pollinator community. This study was intended to illustrate that there could be discriminatory power among sites, and that phytometry was comparatively

Table 3 Summary of ranked seed set per inflorescence, from low (1) to high (9–12, depending on plant species) for each test plant species. Values in parentheses are the mean rank for the site, used only if data were missing for that plant species (i.e. it was not deployed at that site or lost in the field due to herbivory or other mortality)

2011	*S. cordifolium*	*S. ericoides*	*S. puniceum*				Sum ranks
EAS	3	1	1				5
BFE	2	3	2				7
WAY	1	4	4				9
CCF	5	2	3				10
GSF	4	5	(4.5)				13.5
2012	*S. cordifolium*	*S. ericoides*	*S. puniceum*	*S. novae-angliae*	*S. oolentangiense*	*S. pilosum*	Sum ranks
CVF-1	(1.75)	2	1	(1.75)	2	2	10.5
EAS	3	3	5	5	1	7	24
TSH	1	1	6	1	7	8	24
WAY	1	5	7	6	3	6	28
BFE	5	(4.8)	1	4	4	10	28.8
GSF	7	(5.8)	4	2	12	4	34.8
GIL-N	4	6	11	3	8	5	37
CVF-2	(7)	(7)	9	(7)	5	(7)	42
LEN-N	9	7	10	9	6	3	44
CCF	6	4	8	7	10	9	44
GIL-A	8	9	12	8	9	1	47
LEN-A	10	8	(10)	10	11	11	60

easy to use as a monitoring tool. Some of the fall-blooming species used reflected pollinator assemblage characteristics, which may or may not be closely related to pollination service delivery throughout the year or at any one time. But since the method is feasible, there is potential for development and extension of the method to particular times of year (i.e. during the bloom of a crop, evaluating reproductive service to a threatened wild plant) or to evaluate particular components of the fauna (i.e. bumble bees, small solitary bees, flies). Using any species of plant will only provide PSM to that species, of course, the goal is comparability among sites, and to do this one must determine what one wishes to compare. However, there is a likelihood that sites with strong pollination service at one time of year are likely to also be strong at other times of year. Inferring

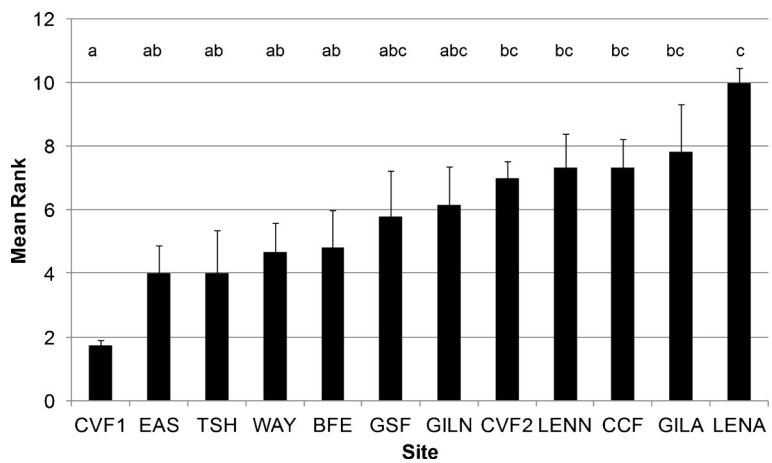

Fig. 4 Sum of seed set ranks across sites for six species of *Symphyotrichum* in 2012. *Bars sharing the same letter code* are not significantly different from one another (GLM, Tukey test, α=0.05). *Error bars* show 1 S.E

ecosystem services indirectly from community variables such as abundance and diversity, guild structure, and so forth is no substitute for direct measurement of the service. In this case, direct measurement is also less costly and labour intensive, which is a cornerstone of the study's rationale.

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Appendix

Table 4 Occurrence of bee taxa at the study sites

Bee species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Agapostemon sericeus	X	X		X	X				X	X	
Agapostemon texanus								X			
Agapostemon virescens	X	X		X		X	X	X	X		
Andrena andrenoides	X				X						
Andrena canadensis				X				X			
Andrena carlini			X	X	X						
Andrena commoda			X		X						
Andrena ?confederata					X						
Andrena ?crataegi										X	
Andrena cressonii					X						
Andrena erigeniae			X		X						
Andrena erythrogaster	X										
Andrena fenningeri					X						
Andrena forbesii					X						
Andrena hippotes			X		X						
Andrena hirticincta	X			X							
Andrena illinoiensis					X						
Andrena imitatrix imitatrix			X		X						
Andrena macoupinensis			X								
Andrena miranda								X			
Andrena nasonii		X	X	X	X					X	X
Andrena ?nigrihirta									X		
Andrena nubecula					X						X
Andrena obscuripennis				X							
Andrena perplexa										X	
Andrena regularis										X	
Andrena rudbeckiae	X	X									
Andrena ?solidaginis	X										

Table 4 (continued)

Bee species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Andrena thaspii				X							
Andrena vicina			X		X						X
Andrena ?wheeleri					X						
Andrena wilkella	X	X	X	X	X	X					
Andrena w-scripta					X					X	X
Anthidiellum notatum		X									
Anthidium manicatum		X		X	X						
Anthophora sp.				X						X	
Apis mellifera	X	X	X	X	X	X			X		X
Augochlorella aurata	X	X	X	X	X	X	X	X	X	X	X
Bombus bimaculatus	X	X		X	X						
Bombus borealis		X	X		X						
Bombus griseocollis			X								
Bombus impatiens	X	X	X	X	X	X	X		X		
Bombus perplexus	X										
Bombus rufocinctus	X	X	X		X						
Bombus sandersoni					X						
Bombus vagans	X	X				X	X	X		X	
Calliopsis andreniformis					X	X					
Ceratina sp.						X	X	X			X
Ceratina calcarata	X	X		X					X	X	
Ceratina dupla	X	X	X	X	X				X	X	
Ceratina mikmaqi	X	X	X	X	X		X		X		
Coelioxys octodentata					P						
Coelioxys rufitarsus		P	P	P	P						
Coelioxys sayi							P				
Colletes eulophi		X		X							
Colletes hyalinus	X										
Colletes mandibularis	X										
Colletes nudus	X										
Colletes simulans	X			X							
Halictus confusus	X	X	X	X	X	X	X			X	
Halictus ligatus	X	X	X	X	X	X	X	X	X	X	X
Halictus rubicundus	X	X	X	X	X		X				
Heriades sp.		X			X						
Hoplitis anthocopoides			X		X						
Hoplitis albifrons					X						
Hoplitis pilosifrons	X	X	X	X	X						
Hoplitis producta				X							X
Hoplitis truncata				X							
Hylaeus sp.	X	X	X	X	X					X	X
Lasioglossum admirandum			X								
Lasioglossum anomalum	X	X	X	X	X						
Lasioglossum atwoodi	X	X	X			X					

Table 4 (continued)

Bee species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Lasioglossum bruneri	X			X		X	X	X			
Lasioglossum cinctipes					X		X	X			
Lasioglossum comagenense				X							
Lasioglossum coriaceum								X			X
Lasioglossm cressonii				X	X				X		X
Lasioglossum dreisbachi	X	X	X	X	X						
Lasioglossum ?ephialtum	X	X		X							
Lasioglossum ?fattigi	X	X				X					
Lasioglossum foxii		X	X	X	X					X	X
Lasioglossum heterognathum	X	X		X	X						
Lasioglossum hitchensi	X	X		X	X	X	X	X			
Lasioglossum imitatum	X	X		X	X				X	X	X
Lasioglossum leucozonium	X	X		X	X	X			X	X	X
Lasioglossum lineatulum	X	X		X	X			X		X	X
Lasioglossum macoupinense	X	X	X	X				X			X
Lasioglossum michiganense	X										
Lasioglossum nigroviride		X				X					X
Lasioglossum occidentale			X		X						
Lasioglossum oceanicum			X		X					X	
Lasioglossum paradmirandum		X			X	X				X	
Lasioglossum pectinatum		X									
Lasioglossum pectorale	X			X	X	X		X			
Lasioglossum perpunctatum	X	X	X	X	X				X		
Lasioglossum pilosum	X	X	X	X	X	X	X	X	X		X
Lasioglossum ?planatum						X					
Lasioglossum platyparum		X									
Lasioglossum pruinosum	X										X
Lasioglossum sagax		X			X					X	
Lasioglossum subversans			X	X	X	X					
Lasioglossum tegulare	X		X	X	X		X				
Lasioglossum tenax		X		X	X		X			X	
Lasioglossum timothyi		X		X	X						
Lasioglossum truncatum								X			
Lasioglossum versans		X		X	X	X					X
Lasioglossum versatum	X	X	X	X	X	X				X	X
Lasioglossum vierecki	X				X	X	X	X	X		
Lasioglossum viridatum										X	
Lasioglossum weemsi	X	X	X	X	X	X		X		X	
Lasioglossum zephyrum					X						
Lasioglossum zonulum				X	X	X					
Lasioglossum ?zophops				X							
Megachile brevis	X	X		X	X						X
Megachile campanulae		X		X							
Megachile centuncularis											

Table 4 (continued)

Bee species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Megachile frigida		X		X							
Megachile gemula		X	X								
Megachile inermis		X								X	
Megachile latimanus		X	X	X	X						
Megachile lippiae		X		X	X						
Megachile mendica	X	X		X	X				X		
Megachile montivaga				X	X						
Megachile perihirta		X					X				
Megachile pugnata	X										
Megachile relativa		X		X	X						
Megachile rotundata	X	X		X	X						X
Megachile texana	X	X		X							
Melissodes ?boltoniae	X	X									
Melissodes communis	X				X						
Melissodes desponsa	X			X							
Melissodes druriella	X	X	X	X	X		X		X		
Melissodes illata				X							
Melissodes subillata	X	X		X	X		X				
Melissodes trinodis	X										
Melissodes ?wheeleri				X							
Nomada sp.		P		P	P						
Nomada articulata	P			P	P	P					
Nomada bethunei	P				P	P					
Nomada cressonii				P	P						
Nomada nr. *cressonii*										P	
Nomada cuneata					P						
Nomada denticulata			P								
Nomada nr.*integerrima*	P										
Nomada luteoloides		P		P							
Nomada nr. *ovata*				P						P	
Nomada nr. *sayi*			P		P						
Osmia conjuncta	X		X	X	X						
Osmia caerulescens		X	X								
Osmia atriventris					X						
Osmia distincta						X				X	
Osmia proxima		X							X		
Osmia pumila				X						X	
Osmia simillima			X		X		X		X	X	
Peponapis pruinosa									X		
Perdita octomaculata	X										
Pseudopanurgus nebrascensis	X	X		X		X					
Sphecodes atlantis	P				P		P		P		
Sphecodes ?banksii	P			P	P				P		
Sphecodes clematidis				P							

Table 4 (continued)

Bee species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Sphecodes confertus	P										
Sphecodes cressonii	P										
Sphecodes ?davisii				P					P	P	
Sphecodes dichrous	P				P						
Sphecodes nr. *dichrous*					P						
Sphecodes ?galerus									P		
Sphecodes heraclei		P									
Sphecodes johnsonii						P		P		P	
Sphecodes ?levis				P							
Sphecodes ?minor				P							
Sphecodes ?nigricorpus									P		
Sphecodes persimilis	P										
Sphecodes ?pycnanthemi				P			P				
Sphecodes ?ranunculi			P								
Sphecodes ?solonis					P						
Sphecodes ?stygius	P	P		P		P	P	P	P		
Sphecodes ?wheeleri		P									
Stelis lateralis	P			P	P						
Triepeolus helianthi	P										
Triepeolus nigrihirtus	P										
Triepeolus ?obliteratus	P										
Triepeolus ?simplex	P				P						
Xylocopa virginica	X	X	X	X	X						
Parasitic bee richness	15	6	4	14	15	4	4	2	6	4	0
Total bee richness	78	73	48	85	93	32	24	21	27	32	24

Table 5 Occurrence of syrphid taxa at the study sites

Syrphid species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Allograpta micrura				X							
Allograpta obliqua	X		X	X	X					X	
Chalcosyrphus metallicus										X	
Chalcosyrphus nemorum	X	X		X	X	X		X		X	
Chrysotoxum pubescens		X		X	X				X		
Epistrophe nitidicolis	X										
Eristalinus aeneus		X			X						
Eristalis anthophorina		X									
Eristalis arbustorum	X	X		X							
Eristalis dimidiata	X		X		X						
Eristalis flavipes	X	X		X							
Eristalis stipator				X							
Eristalis tenax	X	X	X		X						
Eristalis transversa	X	X									
Eumerus sp.		X		X				X	X		

Table 5 (continued)

Syrphid species	BFE	CCF	EAS	GSF	WAY	GIL-N	GIL-A	LEN-N	LEN-A	CVF-1	CVF-2
Eupeodes americanus	X		X		X				X		
Eupeodes pomus			X		X						
Eupeodes sp.	X	X		X		X		X			
Eupeodes volucris		X									
Eurosta solidagnis	X										
Ferdinandea buccata					X						
Helophilus fasciatus	X	X	X								
Heringia salax		X									
Heringia sp.										X	
Lejops sp.			X							X	
Mallota posticata		X									
Melanostoma mellinum		X	X	X	X						
Merodon equestris			X	X							
Microdon tristis		X									
Ocyptamus fascipennis		X	X								
Orthonevra nitida		X									
Paragus haemorrhous				X							
Paragus sp.		X		X	X		X	X	X		
Parhelophilus laetus		X	X								
Platycheirus angustatus			X							X	
Platycheirus hyperboreus			X	X	X	X		X		X	
Platycheirus nearcticus			X		X						
Platycheirus obscurus			X							X	
Platycheirus quadratus	X		X		X	X				X	X
Platycheirus scambus		X	X			X				X	
Platycheirus sp.		X									
Sphaerophoria asymmetrica				X							
Sphaerophoria bifurcata		X									
Sphaerophoria brevipilosa				X							
Sphaerophoria contigua	X	X	X	X	X					X	
Sphaerophoria philanthus	X	X	X	X	X			X			
Sphaerophoria sp.	X	X	X			X	X	X			X
Sphegina petiolata		X									
Spilomyia longicornis	X			X							
Syritta pipiens	X	X		X							
Syrphus rectus	X										
Syrphus ribesii	X		X								
Toxomerus geminatus	X	X	X	X	X	X		X	X	X	
Toxomerus marginatus	X	X	X	X	X	X	X	X	X	X	X
Trichopsomyia apisaon						X					
Tropidia quadrata						X					
Xylota quadrimaculata		X	X								
Total syrphid richness	22	31	24	22	18	10	3	9	6	13	3
Bee+syrphid richness	100	104	72	107	111	42	27	30	33	45	27
Rarefaction estimate (extrapolation of curve)	100.2	108.4	112.5	135.6	163.11	82.3	69.1	74.4	78.8	51.1	125.9

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