Erratum

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Pollination Reservoirs in Lowbush Blueberry (Ericales: Ericaceae)

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Abstract

Pollinator-dependent agriculture heavily relies upon a single pollinator—the honey bee. To diversify pollination strategies, growers are turning to alternatives. Densely planted reservoirs of pollen- and nectar-rich flowers (pollination reservoirs, hereafter "PRs") may improve pollination services provided by wild bees. Our focal agroecosystem, lowbush blueberry (*Vaccinium angustifolium* Aiton), exists in a simple landscape uniquely positioned to benefit from PRs. First, we contrast bee visitation rates and use of three types of PR. We consider the effects of PRs on wild bee diversity and the composition of bumble bee pollen loads. We contrast field-level crop pollination services between PRs and controls four years postestablishment. Last, we calculate the time to pay for PR investment. Social bees preferentially used clover plantings; solitary bees preferentially used wildflower plantings. On average, bumble bee pollen loads in treatment fields contained 37% PR pollen. PRs significantly increased visitation rates to the crop in year 4, and exerted a marginally significant positive influence on fruit set. The annualized costs of PRs were covered by the fourth year using the measured increase in pollination services. Our findings provide evidence of the positive impact of PRs on crop pollination services.

Agricultura que depende de los polinizadores depende fuertemente de una especie—la abeja melífera. Para diversificar las estrategias de la polinización, los productores buscan alternativas. Una reserva de flores muy densa con una gran cantidad de polen y néctar (una reserva de polinización, en lo sucesivo la 'PR') puede que mejore los servicios de polinización por parte de las abejas silvestres. El agroecosistema focal, el arándano bajo, (*Vaccinium angustifolium* Aiton), crece en un campo sencillo que se beneficiaría de las PRs. En primer lugar, contrastamos la tasa de visita de las abejas a lo largo de tres clases de PR. Tenemos en cuenta los efectos de las PRs sobre la diversidad de las abejas silvestres y la composición de la carga de polen de los abejorros. Cuatro años después de establecimiento, contrastamos los servicios de polinización al nivel del campo entre las PRs y los grupos de control. Finalmente, calculamos el tiempo para realizar ganancias. Las abejas sociales prefirieron los cultivos del trébol; las abejas solitarias prefirieron los cultivos de flores silvestres. En promedio, en los campos de tratamiento, las cargas de polen de los abejorros contuvo 37% de polen de la PR. Las PRs aumentaron significativamente las tasas de visita al cultivo en el año 4, y ejercieron una influencia positiva y marginalmente significativa sobre el cuajado del fruto. Utilizando el aumento medido en los servicios de polinización, los costos anualizados de las PRs habían sido cubierto del año 4. Nuestros hallazgos implican que hay un efecto positivo de las PRs sobre los servicios de polinización.

Key words: agroecosystem, crop pollination, pollination reservoir, wildflower planting, wild bee

Insect pollinators benefit an estimated 75% of the world's most valuable crops (Garibaldi et al. 2011) and 35% of food produced by weight (Klein et al. 2007). Although estimates vary, approximately one-tenth of the annual value of global food production is attributable to pollinators (Gallai et al. 2009). Honey bees (*Apis mellifera*

L.) are commonly assumed to provide the bulk of this service—and still do in many intensive large-scale cropping systems. Wild bees also play an important role (Goulson 2003, Greenleaf and Kremen 2006) and in many cases, contribute more to pollination than honey bees (Asare 2013, Garibaldi et al. 2013, Mallinger and Gratton

2015). The disparity between supply and demand of rental honey bee colonies (Aizen and Harder 2009, Rucker et al. 2011) and the subsequently high colony rental costs (Rucker et al. 2011, Bond et al. 2014) motivate growers to conserve wild bees in pollinator-dependent agroecosystems.

Some growers attempt to increase farm-scale wild bee populations by installing on-farm areas of bee forage. These pollen- and nectar-rich plantings have recently been assigned the name pollination reservoirs (hereafter, PRs; Brosi et al. 2008). Studies across the globe provide evidence that on-farm PRs increase crop yields (Carvalheiro et al. 2012, Blaauw and Isaacs 2014, Barbir et al. 2015, Pywell et al. 2015), attract wild bees (Carvell et al. 2007, Haaland et al. 2011, Scheper et al. 2013, Williams et al. 2015), and increase their diversity (Ponisio et al. 2015), population size (Wood et al. 2015a), stability (M'Gonigle et al. 2015), and populations in surrounding farmland (Morandin and Kremen 2013, Feltham et al. 2015). However, not all studies report positive results (Sardiñas and Kremen 2015, Wood et al. 2015b) and only a few determine whether PRs aggregate bees or function as a source, contributing to wild bee population-level increases (Morandin and Kremen 2013, M'Gonigle et al. 2015, Wood et al. 2015a). Pollinator conservation policy has a rich history in Europe (Osborne et al. 1991, Westrich 1996, Batáry et al. 2015, Dicks et al. 2015). The United States is newly committed to creating or enhancing seven million acres of pollinator habitat (The White House 2015). Better understanding of the impact of PRs in specific crops will allow growers and conservationists alike to implement these strategies where they can be used to greatest effect.

Lowbush blueberry (*Vaccinium angustifolium* Aiton) is a low-growing, woody perennial native to North America. It is predominantly clonal when managed, enabling rapid colonization of the exposed shallow soils typical of Maine and the Canadian Maritimes blueberry barrens. Sexual reproduction of lowbush blueberry is more complex. Clones are largely self-incompatible due to early-acting inbreeding depression (Bell et al. 2009). Plants produce larger fruit and greater numbers of viable seeds when outcrossed (Stubbs et al. 2007, Bell 2009), which is facilitated by bees. The lowbush blueberry agroecosystem is completely pollinator dependent (Eck 1988, Free 1970); bagged flowers are virtually incapable of producing fruit (Stubbs et al. 2007, Bell 2009). Individual fields are typically pruned or burned every other year and harvested on a biennial basis. Growers manage fields along a scale from highly intensive (where aerial pesticide sprays, fertilizers, and irrigation systems are regularly employed) to low-input and organic systems that are virtually unmanaged. Lowbush blueberry contributes US$250 million to Maine's economy every year (Smith 2004) and is an important source of revenue for rural communities. Honey bee colony rental prices paid by lowbush blueberry growers are on the rise (Stubbs and Drummond 2001, Hanes et al. 2013) and when stocked at the recommended rate, colony rentals can account for 35% of lowbush blueberry growers' total variable costs (A.K.H., unpublished data). These costs drive the search for less expensive pollination models that may offer lowbush blueberry growers a partial replacement for rental honey bees.

Historically, wild bees provided all pollination services in lowbush blueberry and they still play a major role today. Two of the most dominant genera of the crop's wild bee pollinators (*Bombus* spp. and *Andrena* spp.; Bushmann and Drummond 2015) are four times more effective pollinators of lowbush blueberry than honey bees (Javorek et al. 2002). During blueberry bloom overwintered bumble bee queens forage in blueberry fields. Queens release sticky pollen from the plant's poricidal anthers via buzz pollination. Subsequent flower-visiting honey bees seem to receive a dusting of

pollen from the pollen-covered flower, enhancing their pollination efficacy to this and subsequent flowers (Drummond 2016).

In many of the smallest fields, wild bees provide 100% of pollination needs. The wild bees associated with the lowbush blueberry agroecosystem have been extensively documented (Stubbs et al. 1992). Most recently, Jones et al. (2014) and Bushmann and Drummond (2015) documented over 100 bee species (including kleptoparasites) associated with the crop. Lowbush blueberry fields are typically surrounded by a forest matrix lacking abundant season-long sources of pollen and nectar (Groff et al. 2016). In this landscape, the creation of PRs should create a sharp ecological contrast. Pollination reservoirs positively affect bee communities in relation to the level of ecological contrast between the PR and the surrounding landscape (Scheper et al. 2015).

To our knowledge, this study is the first to examine the effects of PRs in lowbush blueberry, and one of very few in the United States that presents comprehensive findings on the influence and impact of PRs on pollinators and the crop. Our intent is twofold. First, we present a study contrasting different types of PRs and assess their effects on pollination services in crop fields. Last, we consider return on investment of PRs under whole-farm budget scenarios.

Materials and Methods

Effects of Pollination Reservoirs

In June 2012, we established PRs at four sites in Maine. Two sites (fine sandy loam) are owned and operated by commercial lowbush blueberry growers in Blue Hill, Hancock Co., ME (soil pH 4.5 and 5.4). The third, Blueberry Hill in Jonesboro, Washington Co., ME (gravelly sandy loam, pH 5.8), is a University of Maine lowbush blueberry research farm. A fourth site, Rogers Farm Forage and Crop Research Facility in Stillwater, Penobscot Co., ME, also owned by the University of Maine (fine sandy loam, pH 6.1), is composed of hay pasture, annual grains, and mixed vegetables. Rogers Farm is representative of the landscape that surrounds lowbush blueberry fields in the central coast blueberry production region of Maine (Yarborough 2009). All PR treatment sites ($n = 3$) were paired with a control ($n = 3$), which consisted of a nearby (1.5–20 km), similarly managed lowbush blueberry field without PR treatments. Most fields were managed as split-fields, with half of the crop blooming on even years and half on odd years. Some crop fields were not on alternate-year management, and so some treatment sites had multiple nearby control sites that we monitored in alternate years.

The planted area at each treatment site included three 3.3- by 50.0-m treatments: natural regeneration, clovers, and wildflower. All treatments were immediately adjacent, forming a contiguous PR area of 10 by 50 m. At one private farm in Blue Hill, Maine, space restrictions allowed only 100 m^2 of wildflowers, 100 m^2 of clover, and 25 m^2 of natural regeneration. Natural regeneration treatments were not seeded; all plants emerged from the existing seed bank. For a list of sown species and seeding rates, see Tables 1 and 2. We selected plant species by first compiling a literature-based list of the flowering plants known to attract pollinators (Stubbs et al. 1992, Stubbs and Coverstone 2004, Tuell et al. 2008, Mader et al. 2011). Invasive species were removed, keeping only those that were either native or naturalized in Maine. The list was filtered again by pH status, in favor of plants tolerant of the acidic soils in this cropping system. Additional filters included habit, flowering phenology, pollen and nectar content (Loose et al. 2005), nitrogen-fixing status, longevity, and corolla depth. Last, we provided our filtered list to cooperating growers, who removed anything that was perceived as a

Table 1. List of sown species, habit, and seeding rates for wildflower PR treatment

Common name	Species	Habit	No. live seeds/m^2	No. live seeds/ha
Plains Coreopsis	*Coreopsis tinctoria*	Annual	102.8	168,349
Indian Blanket	*Gaillardia pulchella*	Annual	82.5	135,003
Sunflower	*Helianthus annuus*	Annual	29.6	48,562
Lavender Hyssop	*Agastache foeniculum*	Perennial	56.9	93,240
Lance-Leaved Coreopsis	*Coreopsis lanceolata*	Perennial	62.3	101,981
Canada Tick Trefoil	*Desmodium canadense*	Perennial	19.6	32,051
Purple Coneflower	*Echinacea purpurea*	Perennial	50.5	82,718
Common Boneset	*Eupatorium perfoliatum*	Perennial	38.0	62,160
Bergamot	*Monarda fistulosa*	Perennial	43.2	70,707
New-England Aster	*Symphyotrichum novae-angliae*	Perennial	48.7	76,642
Common Oats	*Avena sativa*	Annual	–	10.89 lbs[a]
		Total Wildflower:	534.4	874,412

Except *A. sativa*, statistics shown are supplied by Diane Wilson at Applewood Seed Company. All seeds are organically certified.

[a] *Avena sativa* shown as lbs/acre and not included in live seed totals.

Table 2. List of sown species, habit, and seeding rates for clover PR treatment

Common name	Species	Habit	kg/ha	US$/kg
Crimson Clover	*Trifolium incarnatum*	Annual	7.8	17.53
Medium Red Clover	*Trifolium pratense*	Perennial (short-lived)	5.6	20.94
Sweet Yellow Clover	*Melilotus officinalis*	Biennial	6.7	18.08
		Total Clover:	20.2	56.55

Pricing is from Johnny's Selected Seeds 2012 prices. All seeds are organically certified.

potential weed (e.g., *Chamerion angustifolium* L. and *Asclepias syriaca* L.). In addition to our treatments, sites contained an adjacent plot with 36 different bee forage plants (6.1 by 6.1 m) as part of a separate study. In total, we added less than 0.05 ha of PR to each site, comprising 1–5% of the total cropped area. PRs were located near fields surrounded by 7–25% lowbush blueberry land within 500 m and which ranged in size from 3.5 to 21.8 ha.

Between 18 May and 1 June 2012, we prepared the seedbed. Seeds were sown in accordance with the methods of Mader et al. (2011) and Blaauw and Isaacs (2014) (for specifics see Venturini 2015). Oats were hand broadcast as a nurse crop in the wildflower treatment only. Planting dates ranged from 8 June to 20 June 2012. During seedling establishment, plots were watered as needed. Excepting natural regeneration plots, the tallest weeds were line-trimmed during the first year when weeds were significantly taller than sown seedlings. These PR and control sites were used to assess the impact of PRs on pollination services and on the composition of bumble bee pollen loads. The PR treatment sites alone were used for comparisons of the three different PRs: clover, wildflower, and natural regeneration. Detailed labor and expense records were kept at every stage of the planting process in order to develop an enterprise budget model for PRs.

Bee Visitation Within Treatments

We sampled bee visitation at two treatment sites late in 2012 during the first year of bloom. Rogers Farm was sampled on 20 and 23 July 2012; Blueberry Hill was sampled on 23 July, 6 July, and 13 September 2012. In 2013, we sampled all four treatment sites every two to three weeks from June to September 2013, with a break for lowbush blueberry harvest in August.

Three representative 1.0-m^2 quadrats of each of the three most dominant blooming species in each treatment were observed for 1-min periods, for a total of 9 min per treatment per sampling date. To reduce edge effects, all quadrats were placed ≥1.0 m from the plot edge. In treatments that contained fewer than three blooming species, we apportioned observations according to floral abundance. Flower visitors were grouped to morpho-species, and for some analyses by sociality, with *Bombus spp.* and honey bees as social, and all other species designated as solitary. We used a Kestrel weather meter (Model 3500, Birmingham, MI) to record weather data during each site visit. Voucher collections were used to estimate accuracy of on-the-wing identification (Supp. Table 1 [online only]). To limit collections, specimens from separate bumble bee pollen load analyses were used as vouchers for the category "bumble bee" (all *Bombus* species except *Bombus ternarius* Say) and for *B. ternarius*. Although it is possible to mistake *B. ternarius* for the rarer *Bombus rufocinctus* Cresson, the latter species did not occur in our 235-specimen bumble bee voucher collection. We did not distinguish commercial bumble bees from wild conspecifics, as it is usually not feasible. The identities of all collected species were confirmed or corrected by Sam Droege at the Patuxent Wildlife Research Center, Beltsville, MD. All specimens are deposited at the Maine State Museum Archives in Augusta, Maine.

Floral density can be a primary determinant of bee visitation (Dibble and Drummond 1997, Ohashi and Yahara 2001, Bushmann and Drummond 2015). We recorded floral density within each bee visitation quadrat. When inflorescences were too numerous to count, absolute density was estimated by subsampling (see Venturini 2015). The flowering unit varied with plant species. For example, although *Coreopsis tinctoria* Nuttall is a member of the Asteraceae with capitula, each floret was not counted on each flower head; instead, the sampling unit was the inflorescence.

We also assessed floral density in PRs independent of visitation observations. At all treatment sites, floral density of PR treatments was measured two to three times per week from June through September in 2013 using a transect survey method (Karem et al. 2010). A 3.3-m string was placed diagonally across each PR treatment. To minimize edge effects, all string transects were >1.0 m from plot edges. This was replicated three times within each treatment for a total of nine transects per site visit. If any part of a blooming plant crossed the string's vertical plane, we counted the

number of in-bloom inflorescences on that plant. Methodology varied depending on the arrangement and size of the inflorescence. To convert the linear transect to an absolute estimate of inflorescences/m^2, we measured the diameter of the aboveground portion of five representative plants of each species. These were averaged and used to calculate the sampled area (SA) of each plant species (n) using the formula below, where d = average diameter of the plant species. The constant 3.33 is the length of the string transect.

$$SA_n = (3.33 \times 2d_n) + (\pi d_n^2) \qquad (1)$$

For each site visit in 2013, the number of bees/inflorescence/min was multiplied by the number of inflorescences/m^2 (as estimated by transect counts) to estimate the number of bees/m^2/min. This metric was calculated for the treatments as a whole and also for each plant species observed. Values were pooled to evaluate bee usage of treatments across the entire season. Across-year comparisons were completed using bees/m^2/min, and unlike the independent analysis of 2013 visitation data, did not include floral density.

We analyzed differences between years using visitation by "wild bees" (all bees except honey bees) as the response variable and considered only two sites visited in both years (Rogers Farm and Blueberry Hill). We analyzed the square root transformed metric (bees/m^2/min) using a repeated measures two-way Multivariate Analysis of Variance (MANOVA) with site as the blocking term and natural regeneration, wildflower mix, and clover as treatments.

To better understand differences between treatments, we also considered the more robust 2013 bee visitation dataset independently. We considered the effects of floral density by including only those observations with a paired floral density estimate (transect method). Rare flowering plants were typically not captured by floral density transects. Paired density-visitation observations were pooled by sampling date, leaving 91 different bee density measurements, each of which is comprised of three or more visitation observations.

We pooled bee use of PRs (bees/m^2/min) over time by treatment across the 2013 season and blocked by site. Bees were grouped as wild bees (inclusive of all wild bee categories), solitary bees, honey bees, hover flies, or bumble bees. Two nested groups within the solitary bee category, small black bees and medium striped abdomen bees, were also analyzed. Due to the low number of replications in our Randomized Complete Block Design (RCBD) (4 sites) and the possible low statistical power, we used blocked nonparametric Kruskal–Wallace tests for the overall model analyses and for pairwise comparisons, nonparametric Wilcoxon Block tests. Analyses were performed on JMP version 12 (SAS Institute Inc., 2009 Cary, NC).

Pollinator visitation data were ordinated using nonmetric multidimensional scaling (NMDS). Similar approaches have been used to illustrate bee-flower relationships (Scriven et al. 2013, Wilson et al. 2015). To reduce the effect of low occurrence visits we omitted plant species for which we had < 5.0% of all observations. Plant species that presented abundant flowers at sites and established well were more likely to be observed. Because of this threshold, our observations were limited to *Coreopsis lanceolata* L., *C. tinctoria*, *Melilotus officinalis* L., *Monarda fistulosa* L., and *Trifolium pratense* L.

The main matrix in the ordination contained insects/m^2/min observational data partitioned into the insect categories observed in the field: honey bee, small black bee, medium striped abdomen, hover fly, bumble bee, and other bee. These data were logarithmically transformed for a randomized Monte Carlo test (Barnard, 1963). The second matrix included the following log (x) transformed environmental gradients: number of inflorescences within a 1.0 m^2 quadrat, wind speed, temperature, and relative humidity.

The second matrix also included the two categorical grouping variables, site and plant species.

NMDS ordinations were performed using PC-ORD according to the methods of Mather (1976) and Kruskal (1964). Distances were measured using a Sorensen (Bray-Curtis) approach, starting with a maximum of 6 dimensions and stepping down by 0.20 per iteration with 50 runs using real data. Pairwise comparisons of grouping variables were conducted using a Multi-Response Permutation Procedure (MRPP) in PC-ORD version 6.0 (McCune and Mefford 2011).

Pollination Services in the Crop Field

In the 2012, 2013, and 2015 growing seasons, we measured the influence of PRs on wild bee pollination services. At all sites with paired PR and control fields ($n = 6$), we measured fruit set and visitation rates to blueberry flowers. In each field, we measured fruit set on 48 stems and 12 clones (4 stems per clone) and observed crop flower visitors in 12 blooming clones (1.0 m^2 quadrats). Clones are visibly distinct and were distinguished by morphological differences (e.g., height and color). All clones and quadrats used for quantifying pollination services were evenly distributed throughout the field. In 2012 excessive rain made it difficult to sample visitation to the crop at Blueberry Hill. In 2013, the fruiting-year field was too distant (>400 m) from the planting at one treatment site, and pollination services there were not measured. We collected no data in 2014. All pollination service sampling was measured on the whole-field scale, with quadrats (visitation), and stems (fruit set) distributed throughout the entire crop area.

Fields were visited twice per year in 2012 and 2013 to collect bee specimens for diversity indices. We did not sample bee diversity in 2015. Spring collections were conducted in the crop field during bloom (June). Summer collections (August) were conducted in the available forage in and around each crop field; in PR treatment fields this includes the PR itself. We hand-collected bees in 50-ml centrifuge tubes for a total of one person-hour per field. Collectors walked at a brisk pace to cover as much ground as possible and ensure that collections were representative of the site as a whole. We did not collect honey bees or *Bombus* spp. queens. Sampling was done on clear days between 9:30 am and 4 pm with temperatures between 15 and 30 °C. All species determinations were verified by Sam Droege at the Patuxent Wildlife Research Center, Beltsville, MD. Shannon–Wiener diversity indices and richness were calculated using an online diversity calculator at (Chang Bioscience: www.chang bioscience.com/genetics/shannon.html, accessed 25 November 2016).

A Randomized Complete Block (RCB) Analysis of Variance (ANOVA) was used to determine if the presence of adjacent pollinator plantings had any effect on wild bee density and fruit-set. Site level means comparisons were performed with Student's t-tests. Changes in the bee community (genus diversity, richness, abundance, and evenness) over time were assessed using two-way ANOVA. All statistical analyses in the section above were performed using JMP version 12 (SAS Institute Inc., Cary, NC).

Bumble Bee Pollen Loads

At all sites, two bumble bee collections were made each year (2012 and 2013). We sought to collect 30 bumble bee workers per site per year. Collections were made immediately following blueberry bloom (late June) and in late August. Bees were captured only if pollen loads were visible. At sites with few bumble bees it was not always possible to collect 15 specimens. Workers were often found concentrated in densely flowering areas and were simply caught where they

were found. When possible, paired sites were sampled on the same day. Specimens of all blooming flowers were collected from each site during each collection, identified to species, and used as pollen reference samples.

Both reference samples and pollen loads were processed using acetolysis according to the methods of the University of Maine Palynology Laboratory (see Venturini 2015 for details). Acetolysis procedures were modified from Erdtman (1960) and Jones (2014). Reference sample pollen was processed in a similar fashion and stored in the permanent pollen collection at the University of Maine's Climate Change Institute.

Processed pollen samples were mounted on slides and examined with light microscopy under 40X magnification. Pollen grains were identified to the lowest taxonomic level possible and binned into taxa groups (Supp. Table 2 [online only]). At least 100 pollen grains were identified from each specimen. Grains were identified and counted in transects across slides (Jones 2014) but counting ceased upon transect completion if the cumulative pollen count met or exceeded 300 grains. If the sum of two slides from a single bee specimen was less than 100 grains, the sample was discarded.

The proportion of pollen taxa abundance within each sample was calculated by volume, which is a more direct measure of its worth to bees than the number of grains (Da Silveira 1991). Polar and equatorial pollen grain diameters were averaged from measurements of 30 reference pollens for each species. If reference samples were not available, we used previously published average diameters (Reille 1990, Kapp et al. 2000).

To analyze the pollen load species composition, we used unbounded traditional EMS standard least squares (LS) regressions (JMP version 12, SAS Institute Inc., Cary, NC). Dependent variables included pollen diversity, richness, evenness, and the volume-corrected relative abundance of pollen within each load, square root transformed. These data were pooled by pollen type (PR, unsown, and overlap). PR pollen was produced by experimentally sown flowers in treatments, unsown pollen was produced by naturally occurring plants in the natural regeneration treatment, and overlap pollen was *T. pratense* and *Trifolium incarnatum* L., which occur as both sown and unsown plants in our study sites. The main model effects were year, season (early and late), treatment (control and treatment), treatment × season, treatment × year, crop field size, and crop field size × treatment. Random effects were season × year and treatment × season × year. We used a Student's t-test of LS means to determine specific patterns in the interaction.

Pollination Reservoir Economics

At three sites, budgets were constructed from our records of labor, fuel, and equipment costs incurred during PR establishment and maintenance. Both variable costs (e.g., labor and fuel, seed and lime for PR, pesticides for crop) and fixed costs (e.g., equipment depreciation, fixed cost of land) were calculated. Lowbush blueberry net farm income (NFI) was calculated as total crop revenue minus variable costs minus fixed costs. One-time variable costs for PRs (e.g., seed) were annualized over four years. Four years is a conservatively short estimate of the effective life of PRs (Venturini 2015). Other variable costs (e.g., labor and fuel for annual mowing) were incurred each year. Fixed equipment costs were depreciated over the useful life of each implement.

Establishment costs of PRs were paid off over time by either the PR-attributed increase in crop profit or NFI. Similar to the methods of Blaauw and Isaacs (2014), increases in crop yield were calculated from the marginally significant increase in fruit set from PRs. Time

Table 3. Timeline of sampling

	2012					2013					2015				
	VCF	FS	PR	H'	BP	VCF	FS	PR	H'	BP	VCF	FS	PR	H'	BP
PR															
Field A	x	x	–	x	x	x	x	x	x	x	x	x	–	–	–
Field B	x	x	–	x	x	x	x	x	x	x	x	x	–	–	–
BBHF	–	x	x	x	x	x	x	x	x	x	x	x	–	–	–
Roger's	–	–	x	x	x	–	–	x	x	x	–	–	–	–	–
Control															
Field C	x	x	–	x	x	–	–	–	–	–	x	x	–	–	–
Field D	–	–	–	–	–	x	x	–	x	x	–	–	–	–	–
Field E	x	x	–	x	x	x	x	–	x	x	x	x	–	–	–
Field F	x	x	–	x	x	x	x	–	x	x	x	x	–	–	–

VCF denotes visitation by bees to crop flowers. FS denotes crop fruit set. PR refers to all sampling activities (floral density and bee visitation) conducted in PRs. H' denotes hand collections of wild bees for diversity samples. BP denotes collections of bumble bees with pollen loads for pollen analyses. Roger's Farm is not a blueberry field and so has no control. BBHF refers to Blueberry Hill Farm. Field D replaced Field C in 2013 due to crop failure. Privately owned fields are not named to respect privacy.

to reach positive profit was examined under four scenarios: PR-attributed yield increase and NFI; seed costs covered by NRCS; higher revenue (US$0.51/dry liter) from greater consumer willingness to pay for native bee pollinated blueberries (Stevens et al. 2015); and forgone income from crop area converted to PR. NFI is based upon the typical lowbush blueberry split-field scenario. Only one-half of the biennially harvested crop is harvested each year.

We used NFI for one of the four scenarios we present. NFI equals crop revenue (US$/ha) minus annual total (variable + fixed) costs (US$/ha of lowbush blueberry). Fixed costs include equipment depreciation (e.g., tractor) which is annualized over its useful life. Economic budgets were constructed for crop and PR at Blueberry Hill Farm and the two cooperating farms in Blue Hill, Maine, following standard methodology (Kay 2011). Budgets were constructed in Excel after interviewing cooperating growers. The Blueberry Hill Farm (University of Maine Research Facility) lowbush blueberry budget was engineered to reflect a typical conventional lowbush blueberry farm budget, based upon budget development interviews of 23 conventional lowbush blueberry growers. All interviews took place between 2012 and 2015.

Results

Effects of Pollination Reservoirs

Bee Visitation Among PRs

In 2012, the establishment year, we completed 69 timed observations at two different sites and observed a total of 64 insect visits to flowers from 23 July to 13 September. These observations were distributed over nine different plant species and included 16 visits by wild bees (5 solitary and 11 bumble bee visits), no visits by honey bees, and 48 visits by other insects. In the second year of establishment, from 18 June to 17 September 2013, we completed 570 timed observations in clover, natural regeneration and wildflower treatment plots and recorded 1,325 insect visits comprised of 221 solitary bees (Halictidae, Andrenidae, Megachilidae, Colletidae, and others), 101 honey bees, 259 bumble bees, and 744 wasps, hover flies (Syrphidae), and other insects. A timeline of all sampling activity is given in Table 3.

There were no significant differences in total wild bee visitation rates between years or among PR treatments ($F_{(3,2)} = 1.43$,
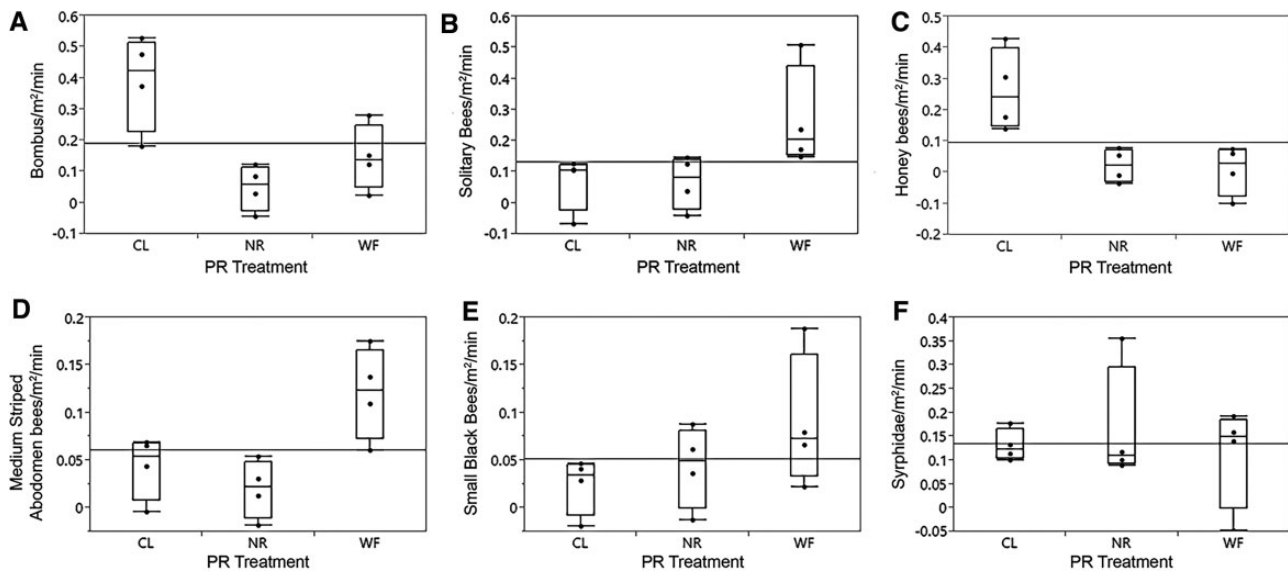
Fig. 1. Mean 2013 bee visitation rates in PR treatments. Data represented by box plots, first and third quartiles are box edges, bars denote minimum and maximum, points refer to replicates (sites). Horizontal lines within boxes are mean densities of (**A**) Bombus spp., (**B**) solitary bees, (**C**) honey bees, (**D**) medium striped abdomen bees, (**E**) small black bees, and (**F**) Syrphidae. Group designations are from on-the-wing identifications. Composition of group designations is available in Supp. Table 1 (online only). X-axis abbreviations refer to the PR treatments, clover (CL), natural regeneration (NR), and wildflower (WF).

$P = 0.437$). However, the pattern among treatments was similar in both years. In 2012 and 2013, 0.68 (0.29) and 0.78 (0.15) wild bees/m²/min visited clover, 0.17 (0.05) and 0.27 (0.12) wild bees/m²/min visited natural regeneration, and 0.30 (0.08) and 0.51 (0.11) wild bees/m²/min visited wildflowers, respectively. In both years, natural regeneration treatments were visited the least, and wildflower treatments were visited less than clover.

In 2013 wild bees (solitary and social) used the three plantings at different rates (one-way Wilcoxon/Kruskal–Wallis test, $\chi^2_{(2)} = 5.81$, $P = 0.055$; Fig. 1). Clover was used more than natural regeneration (planned pairwise comparison, $P = 0.030$), but not more than wildflower ($P > 0.05$) and there was no difference among the natural regeneration treatment and the wildflower mix ($P > 0.05$; See methods for a definition of 'use'). Bumble bees used clover the most ($\chi^2_{(2)} = 7.27$, $P = 0.026$). Nonparametric rank comparisons of bumble bee visits revealed a significantly greater use of clover than natural regeneration ($P = 0.030$). Further comparisons of bumble bee plant use were not significant. *Melilotus officinalis* bloomed more prolifically than any other plant (Fig. 2) and bumble bees foraging on it showed a high degree of floral constancy (Supp. Fig. 1 [online only]). Natural regeneration PRs presented an abundance of flowers at some points in the season, although most of these were visited at very low levels, if at all. Figure 2 illustrates the phenology of each PR treatment.

We performed one-way Wilcoxon/Kruskal–Wallis tests on the category, "solitary bees." The wildflower mix was used most, followed by natural regeneration and then clover ($\chi^2_{(2)} = 7.42$, $P = 0.024$) and ranked Wilcoxon comparisons were significant between wildflower and clover ($P = 0.030$), and between wildflower and natural regeneration ($P = 0.030$). There was no difference between bee use of clover and natural regeneration treatments. Honey bee plant use was similar to that of bumble bees ($\chi^2_{(2)} = 7.39$, $P = 0.025$) and honey bees used clover at a much greater rate than either wildflower ($P = 0.030$) or natural regeneration ($P = 0.030$). Medium striped abdomen bees, primarily Halictidae (83.3%), and mostly *Halictus* spp. (66.6%), used the wildflower mix more than natural regeneration ($P = 0.030$) and clover. Small black bees, primarily Halicitidae (91.6%), mostly *Lasioglossum* spp. (66.6%) exhibited no difference among treatments

($\chi^2_{(2)} = 2.46$, $P = 0.292$). Hover flies were frequently observed in all treatment types and exhibited no significant differences among treatments ($\chi^2_{(2)} = 0.27$, $P = 0.874$).

Bee Visitation to PRs by Flower Species
The NMDS ordination of bee visitation to flower species in 2013 resulted in a 3-dimensional solution after 96 iterations, and when compared to a randomization of the data (Monte Carlo test) was significant ($P = 0.020$) with a mean stress of 0.150. Three axes explained 71.5% of the pollinator community variance, with the 1st, 2nd, and 3rd accounting individually for 26.9%, 21.8%, and 22.7% of the total variance, respectively. Pairwise comparisons using a Multi-Response Permutation Procedure revealed that flower visitor communities differed between the following pairs of plants: *C. lanceolata* and *M. officinalis* ($P = 0.033$), *C. tinctoria* and *M. officinalis* ($P < 0.001$), *C. tinctoria* and *M. fistulosa* ($P < 0.001$), *C. tinctoria* and *T. pratense* ($P < 0.001$), and *M. officinalis* and *M. fistulosa* ($P = 0.002$).

Bumble bees and honey bees used flowers similarly, and were separated from other insect visitors in the community of plants that they visited (Supp. Fig. 2 [online only]). They were most exclusively associated with the clovers: *M. officinalis* and *T. pratense*. The solitary bee species group designations medium striped abdomen, small black bee, and other bee were similar to hover flies in patterns of floral visitation and all were centrally located on the ordination axis. These groups were most exclusively associated with *C. tinctoria* and *C. lanceolata* (Supp. Fig. 2 [online only]).

Examination of correlations with the second matrix (environmental gradients) revealed the most likely environmental associated variables for each axis. The first and most significant axis was primarily associated with floral density ($r^2 = 0.13$), signifying that both honey bee and bumble bee visits tended to visit dense patches of inflorescences. Other insect groups were more centrally located on all axes. The main predictors associated with axis 2 included wind speed ($r^2 = 0.03$), relative humidity ($r^2 = 0.02$), and air temperature during observed foraging ($r^2 = 0.01$). Temperature and relative
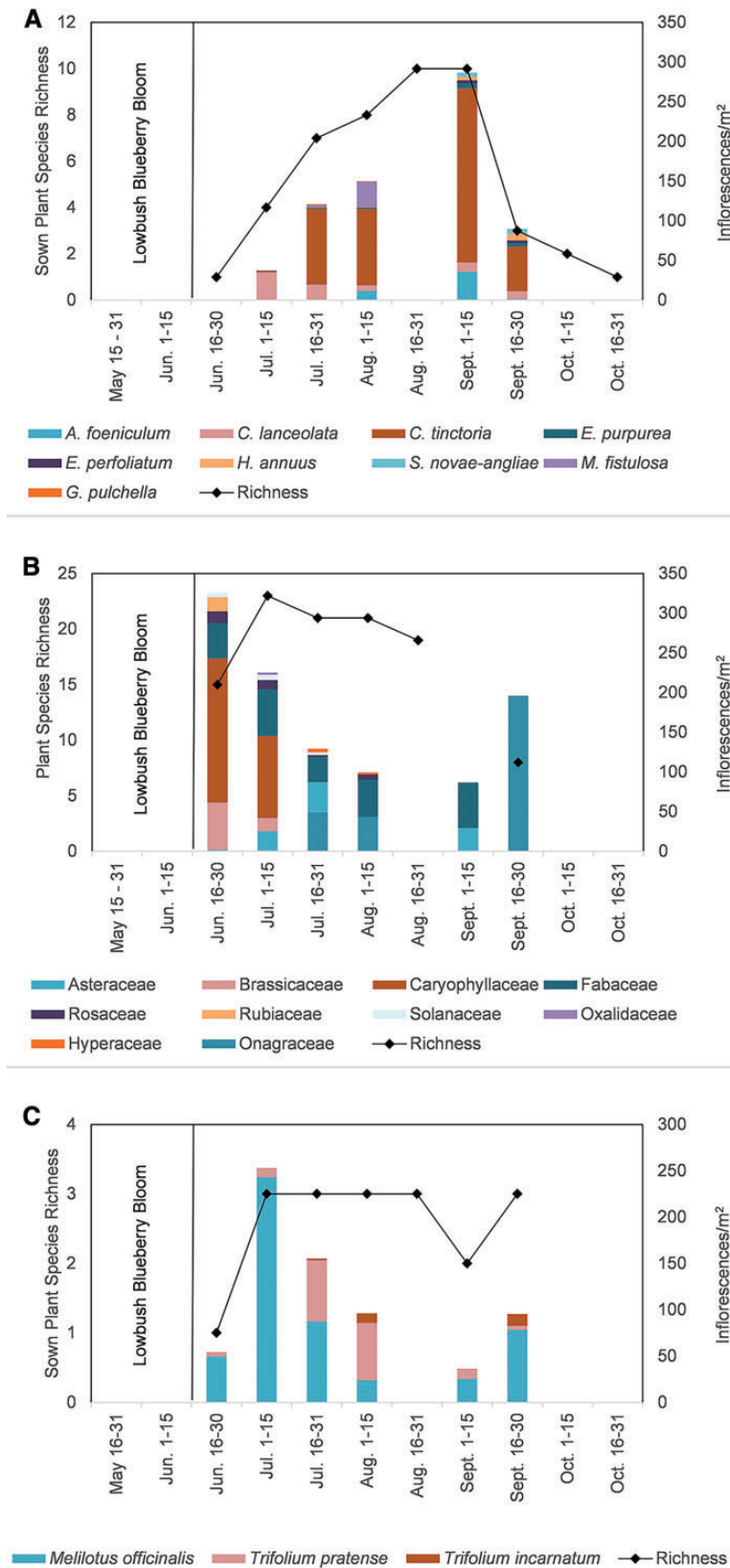
Fig. 2. Phenology and richness of PR treatments in 2013. (**A**) Represents the wildflower mix; (**B**) represents natural regeneration; (**C**) represents clover. Solid black line denotes species richness of sown plants (A and C), or all volunteers (B). In natural regeneration graph (B) bloom is apportioned by plant family instead of species. Inflorescences/m^2 are based on transect surveys. When no transect surveys were conducted (e.g., August 1–15), no bar appears. Richness is based on counts of flowering plants in PRs during each site visit. Lowbush blueberries bloom from mid-May to mid-June, represented by a black outlined box.
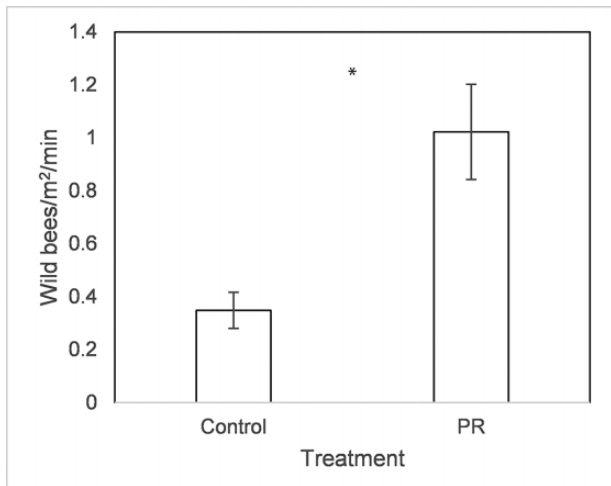
Fig. 3. Abundance of wild bee crop flower visitors in PR versus control fields in 2015. Mean comparison using Student's *t*-test. Asterisk denotes significance at α = 0.05.
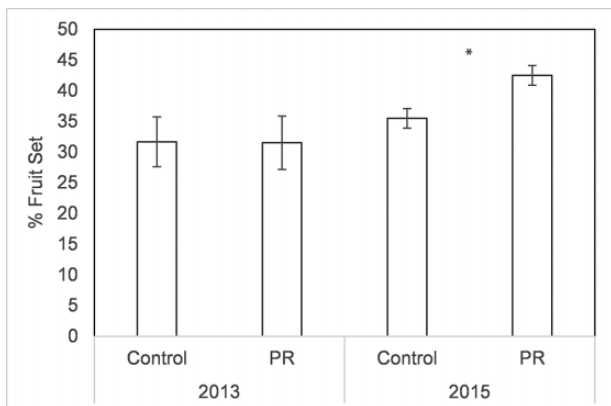

Fig. 4. Fruit-set among PR and control fields in 2013 and 2015. Mean comparison using Student's t-test. Asterisk denotes significance at α = 0.10.

humidity were positively associated with insect visitation rates while wind speed was negatively associated.

Pollination Services in the Crop Field

In 2012 and 2013 wild bee visits to crop flowers were not significantly different between PR and control fields ($F_{(1, 5)} = 0.03$, $P = 0.868$). In 2015 wild bee visitation to crop flowers was significantly greater in PR fields ($F_{(1, 5)} = 48.40$, $P = 0.020$; Fig. 3). Fruit-set was not significantly different in 2013 between PR and control fields (Fig. 4). However, in 2015 we observed a difference at the α = 0.10 level.

We collected a total of 827 bee specimens at all sites, by collecting twice at each site in each of two years. Our collections consisted of 91 species of wild bees in 18 genera. A timeline of all sampling activity is given in Table 3. Our two-factor ANOVA compared changes in bee diversity (Shannon–Wiener Index) over time (early season 2012, late season 2012, early season 2013, and late season 2013) between PR and control fields. We did not collect specimens in 2015. Changes in diversity over time between PR and control fields for the pooled bee groups *Bombus* spp. and non-kleptoparasitic Halictidae were not significant ($F_{(1, 27)} = 0.03$, $P = 0.868$ and $F_{(1, 27)} = 0.06$, $P = 0.519$, respectively). We also tested the diversity metrics richness and evenness for *Bombus* spp., non-

Table 4. Relative abundance of pollen among collected bumble bee pollen loads

Level	Student's T-test[a]	Sample size	Mean (SE)	Effect test (Prob > F)
Relative Abundance of Pollen from PR Plants				
Treatment, Early, 2013	A	38	0.486 (0.033)	<0.0001
Treatment, Late, 2013	B	46	0.258 (0.031)	
Treatment, Late, 2012	B	37	0.196 (0.035)	
Treatment, Early, 2012	C	32	0.051 (0.037)	
Control, Late, 2013	C	46	0.050 (0.036)	
Control, Late, 2012	C	20	0.018 (0.055)	
Control, Early, 2013	C	40	0.001 (0.038)	
Control, Early, 2012	C	37	0.001 (0.034)	
Relative Abundance of Pollen from Sources Outside of PRs				
Control, Early, 2012	A	37	0.999 (0.028)	0.0017
Control, Early, 2013	A	40	0.999 (0.031)	
Control, Late, 2012	A	20	0.999 (0.044)	
Control, Late, 2013	A	46	0.991 (0.029	
Treatment, Early, 2012	A B	32	0.949 (0.031)	
Treatment, Late, 2012	B C	37	0.887 (0.029)	
Treatment, Late, 2013	C	46	0.833 (0.025)	
Treatment, Early, 2013	D	38	0.646 (0.027)	
Relative Abundance of Overlap Pollen[b]				
Treatment, Late, 2013	A	46	0.136 (0.024)	0.6826 NS
Treatment, Late, 2012	A B	37	0.114 (0.027)	
Treatment, Early, 2012	B C	32	0.052 (0.029)	
Treatment, Early, 2013	C	38	0.031 (0.026)	
Control, Late, 2013	C	46	0.016 (0.028)	
Control, Early, 2012	C	37	0.008 (0.033)	
Control, Early, 2013	C	40	0.008 (0.030)	
Control, Late, 2012	C	20	0.006 (0.036)	

[a] Student's T-tests of LS Regression (traditional, unbounded, EMS) effect levels. Letters that are different denote significance. Sample size (N) denotes the number of bumble bee pollen loads within each level. Pollen grain counts are multiplied by average pollen grain size for a volume-corrected metric of proportion.

[b] Overlap pollen is defined as pollen from plants that were growing both PRs and also in nonplanted adjacent habitats.

kleptoparasitic Halictidae, and all wild bees, and detected no significant differences. A full list of the specimens collected can be found in the Supp. Table 3 [online only].

Bumble Bee Pollen Loads

We collected a total of 296 bumble bee pollen loads in 2012 and 2013, 153 from PR fields and 143 from control fields. A timeline of all sampling activity is given in Table 3. We used LS regression to test the effects of PRs on bumble bee pollen load composition. With "Season × Year," and "Season × Year × Treatment" included as random effects in the model, the Random Effect, Season × Year × Treatment & Random interaction was significant ($F_{(1,286)} = 16.91$, $P \leq 0.001$). The greatest proportion of PR pollen in bumble bee pollen loads was found at treatment sites in early summer of 2013 (mean proportion = 0.486) and was significantly greater ($P \leq 0.001$) than the proportion of PR pollen found in any other combination of year and treatment. The second greatest proportion of PR pollen was found late in the season at treatment sites in both 2012 and 2013 (Table 4). In 2012, there was no significant difference between treatment and control sites (Table 4). Across all lowbush blueberry treatment sites in 2013, PR pollen comprised an average of 37.2% of bumble bee pollen loads (excluding overlap pollen).

Pollen diversity and evenness were positively influenced by crop field size ($F_{(1, 286)} = 4.16$, $P = 0.042$) but were not associated with
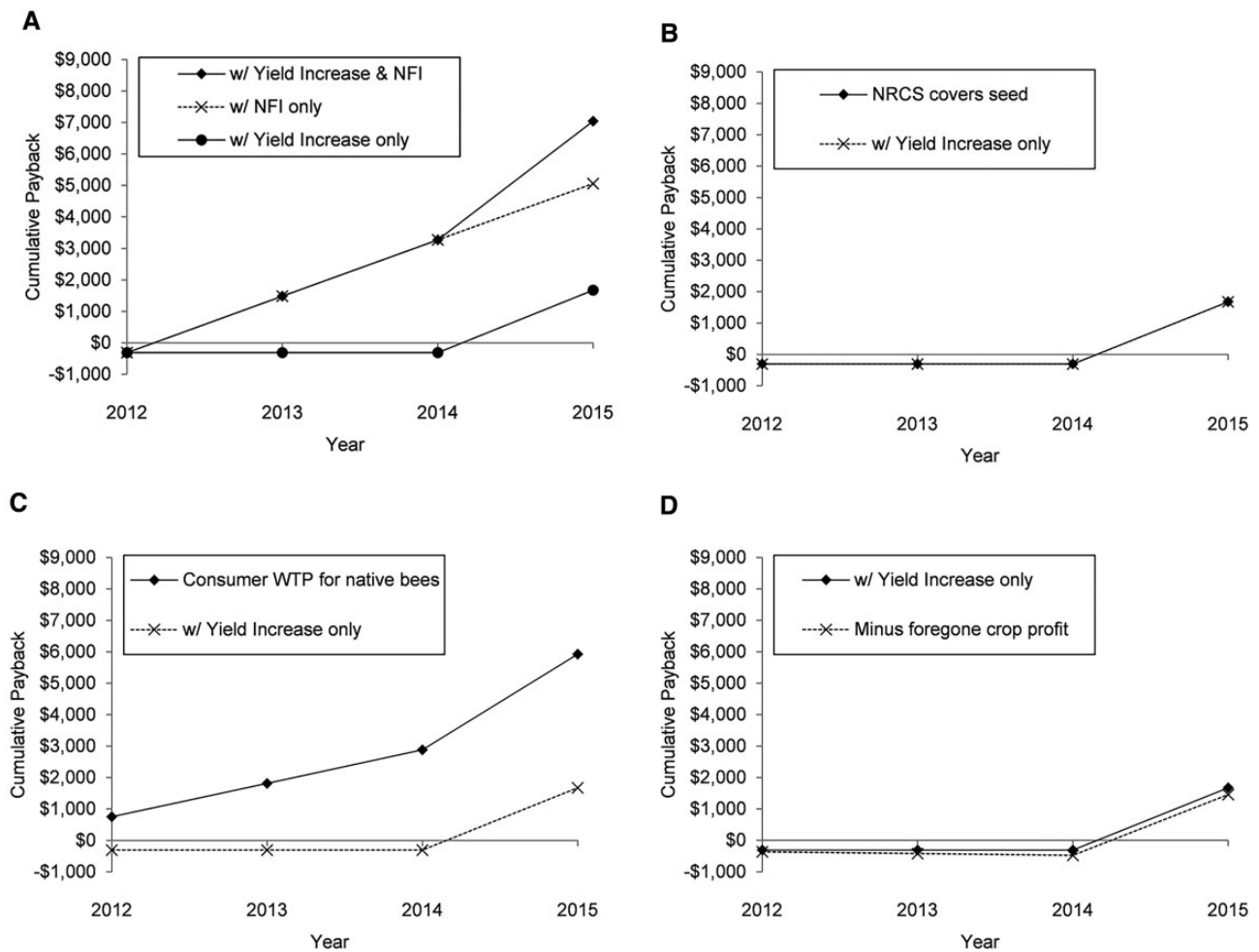
Fig. 5. Average cumulative payback of annual PR (bee pasture) costs (US$/ha) over 4-yr stand life for three on-farm experimental sites. For comparison, "w/yield increase only," is represented in each of the four graphs: (**A**) Includes NFI with and without yield increase and both scenarios are equal with overlapping lines until 2015; (**B**) NRCS covers the cost of seed; (**C**) Consumer willingness to pay (WTP) for native bee conservation practices; (**D**) loss of crop profit from the PR area.

any treatment effects ($P > 0.05$). Species richness of pollen was greater in 2013 ($F_{(1,11.314)} = 46.30$, $P = <0.001$), greater in late season ($F_{(1,0.969)} = 523.02$, $P = 0.031$), and greater in PR fields ($F_{(1,3.088)} = 13.73$, $P = 0.033$). Least square estimates of species richness increased from 2012 to 2013, from 3.420 ± 0.068 (se) to 4.047 ± 0.065, respectively. However, no comparisons yielded significant differences in regard to pollen species richness. Additional tests of pollen load composition data are not presented here (but see Venturini 2015).

Pollination Reservoir Economics

Using only our calculation of the PR-attributed yield increase, payback of establishment and maintenance costs was achieved in the fourth year, the same year as our first record of increased fruit set (Fig. 5A). The average annual lowbush blueberry NFI (US$1,789.35/ha) was more than sufficient to cover the average annual cost of PRs (US$307.62/ha).

Time to payback was only slightly different when NRCS cost share programs covered seed (Fig. 5B). Seed costs comprised a relatively low percentage (5.7%) of annualized PR costs per ha of crop, resulting in a US$7.39/ha average reduction in costs. Based upon consumer surveys, consumers are willing to pay more for native bee pollinated lowbush blueberries (Stevens et al. 2015). If this value is

realized by PRs, blueberry revenues at PR farms would increase by an average of US$1,063.63/ha (Fig. 5C). This increase is large enough to offset PR costs in the first year (2012) of establishment. The foregone profit (NFI) from converting lowbush blueberry land to PR was not substantial (US$49.20/ha of lowbush blueberry on average; Fig. 5D).

Discussion

Effects of Pollination Reservoirs

Bee Visitation Among PR Types

We combined floral density with bee visitation rate into a single metric (use). This allowed us to contrast use by bees per area between PR types—the most relevant metric of comparison to growers. When selecting flowers for inclusion in PRs, their establishment and floral density potential are among the most important factors. Floral density increases bee visitation rates (Smithson and Macnair 1996, Dibble and Drummond 1997, Dauber et al. 2010, Scriven et al. 2013), and certainly influenced visitation rates in our study. While flower preference can only be assessed by controlling for floral density, we did not seek to assess preference. The goal of PRs in an agricultural context is to positively impact the bee community, increasing pollination services and thereby yield. In this context, true preference is less important than use of PRs by bees per

area. Williams et al. (2015) also consider per area use rather than true preference when comparing PRs.

Bees exhibited markedly different use of PR treatments. Clover was used the most, followed by a wildflower mix, and natural regenerating agricultural margins were used the least. Legumes are generally considered excellent bee forage (Decourtye et al. 2010), are frequently cited in regard to honey bees (Campana and Moeller 1977), are often major components of bee flower mixes (Pywell et al. 2011, Wilkerson et al. 2014, Woodcock et al. 2014), and can boost bumble bee populations on a landscape scale (Rao and Stephen 2010, Rundlöf et al. 2014, Wood et al. 2015a). Our results provide additional evidence that clovers are heavily used by bees, especially social bees (i.e., honey bees and bumble bees). Of the three sown species of clover, *T. pratense*, *T. incarnatum*, and *M. officinalis*, the easiest to establish at our sites and the most heavily used was *M. officinalis*. We can attribute this high level of use to its establishment success and floral abundance (Fig. 2) and the high degree of floral constancy apparent in bumble bee pollen loads (Supp. Fig. 1 [online only]). Our analysis of bumble bee pollen loads lends further support to the importance of legumes for social bees.

Wildflower mixtures can offer habitat managers a targeted approach to pollinator enhancement. A diverse mixture of flowering plants with complementary floral morphologies and phenologies benefit a diversity of beneficial insects (Haaland et al. 2011, Blaauw and Isaacs 2012, 2014, Campbell et al. 2012, Fabian 2013, Gill 2013, Korpela et al. 2013, Pywell et al. 2015). Wildflower plant selection can include flowers that target specific pollinator groups, and provide resources during the most critical times. Of the wildflower species planted in this study, several stood out as especially promising. Both species of *Coreopsis*, *C. tinctoria* and *C. lanceolata*, were quick to establish at all sites, bloomed prolifically, and were used extensively by solitary bees. Other studies report similar findings for *Coreopsis* spp. (Tuell et al. 2008, Buckley 2011). *Monarda fistulosa* also established well at a wide range of sites. It attracted a diversity of bees, and was heavily used by bumble bees—as is indicated by the abundance of Lamiaceae pollen in their pollen loads at PR sites. *Symphyotrichum novae-angliae* L. was a prolific bloomer at many sites, but did not begin flowering until late September in each year after sampling was complete. Based on our observations, it was one of the only plants blooming from late September to early October and was so heavily visited by bumble bees during that time that 5–15 individuals were typically foraging on each plant at any given time. Other studies confirm the importance of this aster (Russo et al. 2013).

The natural regeneration strategy is a less expensive, simple way to enhance pollinator habitat in farmland. This technique is appropriate only if opportunity costs (e.g., foregone crop income) are low and if the seedbank is rich in flowering plants (Carvell et al. 2001). In this study, the natural regeneration PR was used less by bees than either wildflower or clover. While some flowers in the natural regeneration PR were visited at high rates (i.e., *Solidago* spp. and *Rubus* spp.), they were less dense than flowers in the planted treatments, and therefore bee densities (per m^2) in natural regeneration plots as a whole were also less. Lowbush blueberry growers in Prince Edward Island, Canada, create similar PRs by cutting back coniferous forest to maintain early successional habitat and 55% of Maine blueberry growers report postponing mowing when wildflowers are in bloom (Hanes et al. 2013). Where growers do not perceive land as limited, large areas of naturally regenerating agricultural margins can offer floral resources and habitat to wild pollinators. However, volunteer plants in naturally regenerating margins are likely to be aggressive agricultural weeds (Wratten et al. 2012), and may pose additional risk.

Our evaluation of PR types was based upon sampling in a single year (2013). This limits our understanding to a short window in the longer-term dynamics of PRs and pollinators. This was the second year after sowing and the year in which clover (esp. *M. officinalis*) bloomed most prolifically. Flowers that establish over a longer period (*Echinacea purpurea* L., *Desmodium canadense* L., *Eupatorium perfoliatum* L.) were not highlighted by our methods. *Echinacea purpurea* bloomed in year two, but at low densities in most sites and *D. canadense* did not fully flower in the first two years, but was one of the most dominant plants in 2015. As the species composition of the wildflower mix changes over time, plants with the longest time to maturity become more dominant, present a greater density of flowers, and become more attractive to pollinators.

Pollination Services in the Crop Field

The effects of PRs on wild bees and pollination services appear to take more than two years to manifest. We did not find differences in fruit set or wild bee diversity between treatment and control fields after only two years. Our findings are supported by several other studies. Blaauw and Isaacs (2014) found measurable effects from wildflower plantings on pollination services in years three and four, but not in years one and two. Pywell et al. (2015) saw no treatment effects of set-asides for the first three years, but effects were apparent from years four through six. Morandin et al. (2016) measured positive effects of 10-yr-old hedgerows on pollination services in California tomato fields. Unlike delayed and incremental population-level effects, the aggregation of bees around a new resource can happen immediately—within the time frame of a single season. Studies of PRs that find increases in bee abundance or pollination services within a single season (Kohler et al. 2008, Barbir et al. 2015, Pereira et al. 2015) are necessarily measuring the effects of aggregation, excepting scenarios where bi- or multivoltine bee species are common. Those that find little to no measureable impact for years are more likely documenting population-level increases (Blaauw and Isaacs 2014, Pywell et al. 2015). Ten-year-old hedgerow PRs in California—likely the most mature PR studied in the US—seem to support such an abundance of pollinators that wild bees are also more abundant in fields near to PRs (Morandin and Kremen 2013). We found no effects of PRs until year four, indicating that measured effects were likely a result of population-level increases, although we cannot be certain.

In the fourth year after establishment (2015), we found positive effects of PRs on pollination services. Wild bee visitation rates were significantly greater in PR fields and fruit set was increased by 10%, although this was only marginally significant at the 0.10 level. This suggests an effect with a 10% probability of being explained by chance. This is not a strong effect, but that is not unexpected considering the relatively small size of the PR: 0.05 ha of PR adjacent to 2.0–4.0-ha fields. Where some studies measured pollination services in a subset of the crop field adjacent to PRs (Blaauw and Isaacs 2014), we measured pollination services over the entire crop field. In Michigan, Blaauw and Isaacs (2014) found positive effects when PRs were 2–32% of the cropped area, but only measured pollination services 15 m into the crop field. Although Blaauw and Isaacs (2014) bagged flowers to account for parthenocarpy in highbush blueberry (*Vaccinium corymbosum* L.), we did not. Unlike highbush blueberry, lowbush is not parthenocarpic and bagged flowers are virtually incapable of setting fruit (Stubbs et al. 2007, Bell 2009). Even our 10% difference in fruit set applied over an entire 2.0–4.0-ha crop field represents a significant yield increase in a pollen-

limited system. Other studies also found measurable field-level changes when relatively small areas were set aside for pollinators. South African mango orchard yields were positively impacted when PRs made up less than 1% of the orchard (Carvalheiro et al. 2012). In England, Pywell et al. (2015) found that flowering set-asides that comprised 3 and 8% of the cropped area exerted positive effects on crop yield, and that effects at 8% were more substantial.

In the lowbush blueberry system of Maine, where fields are often nested within landscapes lacking in flowers, the creation of small, florally dense areas of pollen- and nectar-rich plants create a significant ecological contrast. Landscapes with pre and post PR floral resource disparities are more likely to exert significant effects on pollinator populations (Scheper et al. 2013). Winfree et al. (2007) provide further evidence for the importance of landscape context. They suggest that PRs and other pollinator enhancement strategies should be more effective in homogenous landscapes. Our findings provide one example of the successful use of PRs in agriculturally intensive, homogenous landscapes.

Bees also require nest sites, which can be limiting in some landscapes (Stubbs et al. 1997). Mason, leaf-cutter, and some small solitary bees are cavity nesters. Some occupy the disused tunnels of wood-boring beetle larvae, others nest in hollow stems. Bumble bees are opportunistic, but often take up residence in abandoned rodent burrows. In Maine lowbush blueberry, the abundance of cavity nesters increases when artificial nesting blocks are provided, suggesting that nest sites are limiting for these species (Stubbs et al. 1997). Although in New Zealand bumble bees readily occupied artificial nest sites (Barron et al. 2000), in our cropping system they do not; it is unlikely that bumble bees were limited by nest sites (F.A.D., unpublished data). By far, most wild bees in lowbush blueberry are ground nesters (e.g., *Andrena* spp., *Colletes* spp., *Halictidae* spp.; Osgood 1972, Bushmann and Drummond 2015). It is unclear whether or not soil nesting bees are limited by nesting sites, but lowbush blueberry fields are typically rife with bare patches of soil containing the nest tumuli of (esp.) *Andrena* spp. (F.A.D., E.M.V., unpublished data). It is unlikely that either bumble bees or soil nesting solitary bees are nest limited in our landscape. Converting small areas of turf, forest, or crop field to PR is unlikely to significantly change the distribution of soil nest sites. Cavity nesters on the other hand, are limited by nest sites in our cropping system. Our PRs may have increased the availability of stems for small stem nesters. This addition of nesting sites should not have contributed to the differences we observed in pollination services, as PRs were mowed in the fall. Mowing mortality of stem nesters could render our annually mown PRs a sink, rather than a source, for those species. As PRs continue to become more attractive to growers and conservationists, researchers should seek to understand the wild bee population dynamics associated with nesting sites in PRs.

The installation of PRs may change source-sink and metapopulation dynamics of wild bees in agroecosystems. Species-specific responses to habitat manipulations vary with birth, immigration, and death rates (Pulliam 1988). In bee populations, foraging and dispersal distance, voltinism, reproductive capability, and mortality via kleptoparasites, predation, and pathogens influence birth, immigration, and death rates to regulate source-sink dynamics. The term metapopulation, coined by Levins (1969), is a "population of populations." To date, species-specific population dynamics of most wild bees is unknown, and without these data, their source-sink dynamics are poorly understood. In Sweden, *Andrena humilis* Imhoff populations oscillate biennially for unknown reasons, but metapopulations seem to be driven by classic source-sink population dynamic theory (Franzén and Nilsson 2013). If the *Andrena* spp. associated with

lowbush blueberry show similar population dynamics, the management practices suggested by Brosi et al. (2008), a central large PR and smaller satellite PRs, could be more effective than our approach of a single, small PR. PRs may create source populations, but studies to support this are rare (Morandin and Kremen 2013, M'Gonigle et al. 2015). While PRs in some agroecosystems may create source populations, in other landscapes they may function as sinks due to intensive agricultural practices, or other yet to be understood factors. Our study does little to increase understanding of wild bee source-sink dynamics in agroecosystems. Additional research on species-specific population dynamics is needed to illuminate these dynamics in a PR modified agroecosystem.

This study provides evidence that PRs positively affect pollination services in lowbush blueberry, although the effects take several years to manifest. PRs larger than ours may be needed to more significantly impact wild bee populations, pollination services, and provide partial replacements for honey bees in lowbush blueberry. In other studies, PRs making up of 2–20% of the crop field (Blaauw and Isaacs 2014, Pywell et al. 2015, Wood et al. 2015a) resulted in positive effects (but see Sardiñas and Kremen 2015, Wood et al. 2015b).

Bumble Bee Pollen Loads

Other studies have used comparative analysis of pollen loads to estimate foraging preferences (Stubbs et al. 1992, Kleijn and Raemakers 2008, O'Neill and O'Neill 2011, O'Neill et al. 2012, Pearce et al. 2012). We assessed the contribution of PRs to a surrogate of bumble bee fitness by analyzing the contribution of PRs to pollen loads in PR treatment and control fields. Thirty-seven percent of bumble bee pollen loads in treatment fields were collected from PR plants. This estimate is based on two collections each year, and each collection is a snapshot of the resources that PRs provide bumble bees. The high proportion of PR pollen found in pollen loads suggests that in our study system, small dense plantings can effectively supplement floral resources, and possibly enhance bumble bee populations. This idea is supported by other studies. Sheffield et al. (2008) studied *Osmia lignaria* Say in Nova Scotia and found that populations increased at a greater rate with access to a post crop bloom foraging resource, *Lupinus polyphyllus* Lindley, which is an introduced plant in Maine, and arguably invasive. This species comprised >90% of post crop bloom pollen loads in their study. Alternatively, if PRs were not installed, bumble bee workers may have collected equal quantities of other pollen. In our study, locating bumble bees with full pollen loads was much more difficult in control fields. This suggests that PR pollen is both replacing and supplementing wild pollen sources in the landscape.

Pollination Reservoir Economics

Past studies found significant differences in crop yield and profit as early as the third or fourth year of PR establishment (Blaauw and Isaacs 2014, Pywell et al. 2015). In one case, pollination services were measured 10 years post-establishment, but data from the interim was not presented (Morandin et al. 2016). Time to pay off PR cost can take three or four years for cultivated highbush blueberry with and without a subsidy, respectively (Blaauw and Isaacs 2014). Our time to pay back PR costs in the fourth year should be interpreted with caution as it was calculated using a marginally significant fruit set increase; fruit set is significantly correlated with yield in this cropping system, $r^2 = 0.394$, $P = 0.003$ (Asare 2013). Our estimates are based on a consistent annual yield from a split-field scenario. Although lowbush blueberries are harvested only

every other year, most fields are split, so that roughly half of the acreage is harvested each year. Our economic analysis is slightly different than that presented by Blaauw and Isaacs (2014) in several ways: 1) a lower PR to crop ratio (1:45 versus 1:27); 2) our plantings included clover, which has significantly lower seed costs; 3) their four-year payback assumed that 0.08 ha of PR contributed pollination to 0.18 ha of crop in a 4 ha field (1:2.25 ratio at one field site). We measured pollination services in a larger area representing the entire fruiting field adjacent to PRs (fruiting fields across years averaged 4.9 ha). Despite these differences, we also found that PRs paid for themselves in the fourth year when revenues from estimated yield increases (not crop NFI) were used alone in our calculations. Using crop profits accelerates PR payback to within a year.

We used average crop yields to estimate forgone income from areas converted to PRs. This approach is conservative, as growers tend to site PRs in marginally productive areas, or even in adjacent noncrop areas. Although NRCS subsidies made only a minor contribution to seed costs, most NRCS subsidies are used to pay for expert consultation in planning, design, and installation. We did not include this portion of subsidy monies in our analysis, although expert consultation may increase the positive effects of PRs on yield (see McCracken et al. 2015), and is a requirement of NRCS grants. While consumer willingness to pay for lowbush blueberries pollinated by native bees decreased the pay back PR costs, eco-labeling and certification costs could erode this margin (Stevens et al. 2015). Finally, time to pay back PR cost can be reduced by lower seed costs, higher berry prices, greater cash crop subsidy of PR establishment, or greater wild bee pollination services.

In conclusion, we provide further evidence that PRs can increase pollination services in the crop field, although effects can take several years to be detected. We also provide novel evidence that PRs composed of wildflowers and clovers can provide bumble bees with over 1/3 of their dietary pollen in the second year of establishment, suggesting that PRs exert significant influence on bumble bee colony fitness (Wood et al. 2015a). We did not address the major research gap; what ratio of PR to crop area provides what level of pollination services (Dicks et al 2015)? Our PRs comprised only 1–5% of the cropped area but larger plantings would have likely resulted in a stronger effect. This study supports previous findings that PRs can increase pollination services in crop fields (Kohler et al. 2008, Carvalheiro et al. 2012, Morandin and Kremen 2013, Blaauw and Isaacs 2014, Barbir et al. 2015, Feltham et al. 2015, Ponisio et al. 2015, Pywell et al. 2015), but in a previously untested agroecosystem—lowbush blueberry. Total costs of PRs can be fully covered by the second to fourth year, depending on which metrics are used in calculations. Yet to be demonstrated is the size of plantings required to realize full or partial replacement of managed pollinators in specific agroecosystems.

Acknowledgments

Supplemental Data

Supplementary data are available at *Journal of Economic Entomology* online.

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Erratum

Correction of "Venturini, E. M., F. A. Drummond, A. K. Hoshide, A. C. Dibble, L. B. Stack. 2016. Pollination Reservoirs in Lowbush Blueberry (Ericales: Ericaceae). J. of Econ. Entomol."

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In the online version of this article, the Spanish version of the abstract was incorrectly published as supplementary material. The publisher regrets this error. The text of the abstract is produced below.

"Agricultura que depende de los polinizadores depende fuertemente de una especie—la abeja melífera. Para diversificar las estrategias de la polinización, los productores buscan alternativas. Una reserva de flores muy densa con una gran cantidad de polen y néctar (una reserva de polinización, en lo sucesivo la 'PR') puede que mejore los servicios de polinización por parte de las abejas silvestres. El agroecosistema focal, el arándano bajo, (Vaccinium angustifolium Aiton), crece en un campo sencillo que se beneficiaría de las PRs. En primer lugar, contrastamos la tasa de visita de las abejas a lo largo de tres clases de PR. Tenemos en cuenta los efectos de las PRs sobre la diversidad de las abejas silvestres y la composición de la carga de polen de los abejorros. Cuatro años después de establecimiento, contrastamos los servicios de polinización al nivel del campo entre las PRs y los grupos de control. Finalmente, calculamos el tiempo para realizar ganancias. Las abejas sociales prefirieron los cultivos del trébol; las abejas solitarias prefirieron los cultivos de flores silvestres. En promedio, en los campos de tratamiento, las cargas de polen de los abejorros contuvo 37% de polen de la PR. Las PRs aumentaron significativamente las tasas de visita al cultivo en el año 4, y ejercieron una influencia positiva y marginalmente significativa sobre el cuajado del fruto. Utilizando el aumento medido en los servicios de polinización, los costos anualizados de las PRs habían sido cubierto del año 4. Nuestros hallazgos implican que hay un efecto positivo de las PRs sobre los servicios de polinización."