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Wild pollinators improve production, uniformity, and timing of blueberry crops

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ABSTRACT

Animal pollination is an important input to the global food system, affecting 2/3 of crops and worth more than $100 billion annually. Mounting evidence of pollinators' importance, and of their decline worldwide, has prompted efforts to conserve and restore wild bees within agricultural regions. To date, however, research on the value of wild pollinators has focused largely on crop productivity *per se* and on intensely managed landscapes. Here, we combine field experiments, bee observations, and economic methods to estimate the impact of wild pollinators on the quantity and quality of blueberry crops within a low intensity agricultural landscape in Vermont, USA. Visits by wild bees reduced pollination limitation and increased seed set by up to 92%, fruit mass 12%, and fruit set 12%. Visitation also increased the uniformity of fruit size by up to 11% and advanced the timing of harvest by 2.5 days, both of which can increase crop value. For five out of six groups of wild bees, increased visits improved seed set relative to hand-pollinated controls. The potential economic value of relieving pollen limitation (and therefore improving fruit set and fruit mass) varied widely among farms. On most, production could increase 1–6% (representing $500-$4000 per year in additional revenue), but the maximum increase was 36% (representing $137,000 per year). Conserving wild pollinator communities, therefore, can increase crop quantity, quality, and farm revenue, but some farmers will benefit more than others. Farm-specific studies and recommendations are needed to best inform local and regional management decisions.

1. Introduction

Pollinators represent an essential input to the global food system (Potts et al., 2016). Pollination by bees, birds, bats, and other animals contributes to reproductive success in 88% of the world's flowering plants (Ollerton et al., 2011) and improves yields in roughly two-thirds of crops (Klein et al., 2007). Inadequate pollination in these crops can result in lower and less consistent yields, misshapen fruit, or diminished flavor and quality (Cusser et al., 2016; Garibaldi et al., 2013; Klatt et al., 2014). Crop pollination is therefore a highly valuable ecosystem service, likely worth more than 100 billion dollars per year globally (Breeze et al., 2016; Losey and Vaughan, 2006; Potts et al., 2016).

Although many growers use managed honeybees (*Apis mellifera*) to ensure crop pollination, there is increasing evidence that wild bees play an important role as well (Garibaldi et al., 2013; Gibbs et al., 2016; Ricketts et al., 2004; Winfree et al., 2008). For some crops, native bees are more efficient pollinators than honeybees, depositing more pollen grains per visit to flower stigmas (Javorek et al., 2002). Honeybees and wild bees can complement each other in providing pollination services (Garibaldi et al., 2011; Greenleaf and Kremen, 2006; Rogers et al., 2014; Winfree et al., 2007), and crops appear to benefit from wild bee pollination even when honeybees are abundant (Button and Elle, 2014; Garibaldi et al., 2013).

Managed and wild bees are declining in many regions of the world, due to a mix of parasites, diseases, habitat loss, and pesticides (Bartomeus et al., 2013; Goulson et al., 2015; Potts et al., 2016). The number of honeybee hives in the U.S. declined by 59% over 60 years (National Research Council, 2007), although rates of change differ among regions and countries (Potts et al., 2016). Bumblebees have undergone substantial range contractions and population declines in Europe and North America (Cameron et al., 2011; Goulson et al., 2015). Although data are less available for other regions, several studies document declines outside of North America and Europe (Goulson et al., 2015; Potts et al., 2016).

As part of the response to these trends, there are increasing efforts to conserve and restore wild pollinators. Natural and semi-natural

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habitats, as well as restored hedgerows and wildflower strips, provide nesting habitats and floral resources for bee communities within farmed landscapes (Potts et al., 2016). These habitats can increase the abundance of key pollinators, visitation rate on nearby fields, and resulting crop yields (Blaauw and Isaacs, 2014; Garibaldi et al., 2011; Holzschuh et al., 2007; Kremen, 2005; Ricketts et al., 2008). Although effects vary among regions, settings, and crops (Garibaldi et al., 2013; Kennedy et al., 2013; Kleijn et al., 2015), habitat conservation and restoration is generally an important component of pollinator management.

Despite the many recent studies on the value of wild pollinators to agriculture, our knowledge to date remains limited in two important ways. First, previous studies have focused almost completely on crop productivity (e.g., kg/ha) as the outcome variable of interest. For fruit and vegetable crops, attributes of quality such as appearance, uniformity, flavor, shelf life, and harvest timing also are important in determining commercial value (Dogterom et al., 2000; Gilbert et al., 2014; Klatt et al., 2014). Much less is known about the effects of pollination on these crop attributes (Dogterom et al., 2000; Garratt et al., 2014). Second, most studies have focused on intensely managed landscapes, where honeybees are abundant and nesting and floral resources for wild bees are limited (Blaauw and Isaacs, 2014; Cusser et al., 2016; Klein et al., 2012; Morandin et al., 2007). Fewer studies have focused on complex and less-intensified landscapes (Garibaldi et al., 2016; Nicholson et al., 2017; Winfree et al., 2007), which are typical in many regions worldwide (Fritz et al., 2015). As a result, it is difficult to understand the roles of wild pollinators across the breadth of agricultural systems.

Here, we examine the importance of wild pollinators to both quantity and quality of blueberry crops in Vermont, USA. Blueberries (*Vaccinium corymbosum* L., Ericaceae) in Vermont are grown within a low intensity agricultural system, and are pollinated predominantly by a wild community of native bees (see Methods). Previous work in this same system (Nicholson et al., 2017) found that rates of visitation by wild bees differed more than 10-fold among 15 farms. Variation in visitation rate was significantly explained by three factors: the availability of natural land cover within 2 km of each farm, the management intensity of the farm itself, and the interaction of these two terms.

We build from these results to estimate the yield effects of bee visitation. In nine of the 15 farms, we experimentally measure the degree of pollen limitation (i.e., difference between hand pollinated and open pollinated flowers) on the number, size, uniformity, and timing of harvested blueberries. We then compare farms to quantify the effect of bee visitation on these attributes of crop quantity and quality. Finally, we estimate the potential economic value of additional pollination on each farm, due to increased production (i.e., berry size and number). Our study helps to illuminate the ecological role and economic value of wild pollinators on agricultural outcomes beyond simple yields, in agricultural landscapes that are common worldwide but underrepresented in the literature.

2. Methods

2.1. Study system

Vermont is home to roughly 300 highbush blueberry farms (Keough, 2007), and cultivated acreage has more than doubled in the past 20 years, following national trends (Strik, 2007). Blueberries in Vermont are grown within a lower intensity agricultural system than other regions in the North America. The average farm included in our study is 1.2 ha, compared to 13.8, 10.9, and 8.9 ha for related study farms in British Columbia, Michigan, and Florida, respectively (C. Nicholson and R. Isaacs, unpublished data).

We conducted our study on 9 blueberry farms in Vermont's Lake Champlain Basin (approximate centroid: 44.45 °N, 73.09 °W). Farms cultivated 0.2–2.8 ha of blueberry, typically with a mix of cultivars to extend harvest season. These farms were situated in a gradient of natural landscape composition, with the total proportion of natural area within a 2 km radius ranging from 29 to 86% (Nicholson et al., 2017). All farms grew additional crops, and management practices vary among them. One farm was certified organic, three additional farms strived for low intensity practices, and five practiced conventional agriculture. We focused on one of the most widely grown cultivars in North America (cv. 'Bluecrop'), which is popular for its consistent yield and long harvest season (Draper and Hancock, 1990).

Blueberries require pollination by bees to produce a marketable crop (Klein et al., 2007; Towne, 1995). Yields are reduced 50–80% when bees are excluded from flowers (Button and Elle, 2014), and several studies have found significant pollen limitation on seed set, fruit mass, and fruit set (Benjamin and Winfree, 2014; Button and Elle, 2014; Dogterom et al., 2000). Although many blueberry growers employ honeybees, several native species are more efficient pollinators, in part because of their ability to sonicate (or "buzz") flowers to release pollen (Javorek et al., 2002). In Vermont, Nicholson et al. (2017) found over 80 bee species visiting blueberry flowers. Importantly, honey bees were rare visitors, representing only 13% of individuals observed over 3 years, compared to 74%, 94%, and 89% in British Colombia, Michigan, and Florida respectively (Gibbs et al., 2016) (C. Nicholson and R. Isaacs, unpublished data).

2.2. Pollination experiments

To estimate the magnitude of pollen limitation, we conducted pollen supplementation experiments. In each of the nine study farms, we randomly selected 10 blueberry bushes of the same variety (Bluecrop) and of similar size, branching pattern, and age. Preceding bloom, we selected four branches that were similar in sun exposure, length and number of flower clusters. We assigned each branch randomly to one of two treatments: "open pollination" to measure production under ambient pollination; and "hand pollination", with supplemental pollen applied to flower stigmas by hand. We then counted the number of unopened flowers on each experimental branch.

During blueberry bloom, we visited each farm every 3–5 days to supplement pollination in the hand pollination treatment. We used a VegiBee™ (vegibee.com) to sonicate flowers from nearby bushes and collect their pollen in a Petri dish. We then used a small paintbrush to apply pollen to stigmas of open flowers on all hand pollination branches. Bee visitation rates can vary substantially among blueberry cultivars, due in part to differences in flower morphology (Courcelles et al., 2013). Furthermore, Bluecrop in particular has been shown to exhibit some degree of pollen self-incompatibility (Dogterom et al., 2000). It is therefore uncertain how any hand pollination treatment replicates conditions of pollinator saturation. We address this uncertainty by deliberately mixing donor pollen from several nearby co-flowering bushes, including Bluecrop and other varieties. This approach simulates observed foraging behavior of pollinators, which moved frequently among bushes (pers. obs.) and are likely to carry a similar mix of pollen. We avoided collecting pollen from any experimental bush, to minimize effects on pollination experiments themselves.

Just before harvest began (early July), we counted the number of berries on each experimental branch to estimate fruit set. We then returned to each farm every 3–5 days to harvest any ripe berries from experimental branches. This collection method allows measurement of individual berries, provides information on harvest timing, mimics the harvesting regime in Vermont blueberry farms, and minimizes loss from birds, over ripening, and picking by others. We weighed each berry individually, then counted the number of mature seeds in each under a dissecting microscope. Following Desjardins and De Oliveira (2006), we defined mature seeds as > 1 mm, dark in coloration, with a deeply crenulated seed coat.

From these data, we estimated six response variables that relate to quantity and quality of blueberry harvests: seed set, fruit mass, fruit set, uniformity in seed set, uniformity in fruit mass, and ripening time. We estimated all of these variables for each treatment on each experimental bush. For seed set, we calculated the mean number of mature seeds per berry. For fruit mass, we calculated the mean mass per berry. For fruit set, we divided the number of pre-harvest berries counted in July by the number of flowers counted in May. For uniformity of seed set and fruit mass, we calculated the coefficient of variation (CV) among berries for these variables. For ripening time, we identified the date by which 25% of the berries had been harvested.

For each of the above response variables, we estimated pollen limitation for each experimental bush as the difference between hand pollinated and open pollinated treatments (Kearns and Inouye, 1993). The more pollen limitation departs from zero, the more fruit production or fruit quality is limited by inadequate pollination.

2.3. Pollinator observations

We used pollinator observations published in Nicholson et al. (2017) and summarized here. In 2014 and 2015, we sampled each farm at least three times during four weeks of blueberry bloom, under suitable flight conditions for bees (clear to hazy skies, temperature above 15 °C, and wind speeds less than 3 m/s). For each farm sample, we selected 4 bushes haphazardly from among those in bloom. At each bush, we observed pollinator activity within a $1m^2$ frame of flowering branches for 10 min. We recorded the number of individual bees that visited at least one flower, and the number of flowers each individual visited. Identifying bees consistently is difficult on the wing, so we assigned observed individuals to 8 morphospecies groups (Table 1). We varied time of sampling and observers among farms and sites to avoid bias.

From these pollinator observations, we estimated the mean visitation rate on each farm. We defined visitation rate as the number of flower visits/1 m^2/10 min. For this paper, we focused on wild bees (i.e., all morphospecies other than honey bee (*Apis mellifera*), which were relatively rare visitors).

2.4. Statistical analysis

To test the overall significance of pollen limitation in our system, we calculated the study-wide mean pollen limitation for each response variable in each year. We then conducted one-sample t-tests, testing whether mean pollen limitation = 0. To model the relationships between pollen limitation and visitation rates of wild bees, we calculated mean pollen limitation for each response variable on each farm in each year. We then used mixed effect models with wild bee visitation as a fixed effect and year as a random effect (Zuur et al., 2009). To explore the shape of each relationship, we fit both linear and negative exponential (i.e., Limitation = $a * e^{(-b * \text{Visits})}$) models. We then compared each model to a null model with the fixed effect of wild bee visitation removed, using log-likelihood ratio tests (following a χ^2 distribution). This comparison asks if the full model, including wild bee visitation, describes our data significantly better than a model without this effect. We similarly compared fits of linear and non-linear models using log-likelihood ratio tests and Akaike information criterion (AIC).

2.5. Economic analysis

We estimate economic effects of pollen limitation on blueberry production, by comparing expected yields under conditions of ambient and full pollination. First, we estimated the productivity of each farm, in berries per ha, under ambient pollination conditions (Eq. (1)). On each farm, we counted the number of major stems (hereafter, "canes") on 10 randomly selected Bluecrop bushes. These were not the same 10 bushes used for pollination experiments described above. We then counted the number of berries on four randomly selected canes one week before harvests began. We also measured spacing between rows and between bushes to calculate the number of bushes per ha. Multiplying these three densities gives an estimate of yield (berries/ha).

Table 1
Eight morphospecies groups of bees observed visiting blueberry flowers. For each group, abundances and represented genera and species are listed. Data originally reported in Nicholson et al. (2017) and subsetted here to include only years 2014 and 2015.

Morphospecies	2014 visits	2015 visits	Total visits	Genera represented	Species represented
Bombus (queen)	3366	3098	6464	*Bombus*	*Bombus bimaculatus, Bombus borealis, Bombus fervidus, Bombus griseocollis, Bombus impatiens, Bombus perplexus, Bombus sandersoni, Bombus ternarius, Bombus terricola, Bombus vagans*
Bombus (worker)	155	310	465	*Bombus*	*Bombus bimaculatus, Bombus impatiens, Bombus perplexus, Bombus sandersoni, Bombus ternarius, Bombus vagans*
Black bees (big)	1480	946	2426	*Andrena* *Osmia*	*Andrena carlini, Andrena carolina, Andrena milwaukeensis, Andrena nivalis, Andrena perplexa, Andrena vicina, Osmia bucephala, Osmia cornifrons*
Black bees (slender)	508	434	942	*Andrena* *Colletes* *Osmia*	*Andrena bradleyi, Andrena brevipalpis ♂, Andrena carlini ♂, Andrena carolina ♂, Andrena crataegi ♂, Andrena cressonii, Andrena dunningi ♂, Andrena forbesii ♂, Andrena hippotes ♂, Andrena imitatrix ♂, Andrena integra, Andrena mandibularis, Andrena miserabilis, Andrena nasonii, Andrena platyparia ♂, Andrena rufosignata, Andrena rugosa, Andrena spiraeana, Andrena vicina ♂, Andrena w-scripta, Andrena wilkella, Colletes inaequalis, Osmia albiventris, Osmia inermis ♂*
Black bees (tiny)	271	101	372	*Andrena* *Ceratina* *Halictus* *Lassioglossum*	*Andrena nasonii ♂, Ceratina calcarata ♂, Ceratina dupla, Lasioglossum acuminatum, Lasioglossum birkmanni, Lasioglossum coeruleum, Lasioglossum coriaceum, Lasioglossum cressonii, Lasioglossum ephialtum, Lasioglossum foxii, Lasioglossum heterognathum, Lasioglossum hitchensi, Lasioglossum imitatum, Lasioglossum leucocomum, Lasioglossum lineatulum, Lasioglossum macoupinense, Lasioglossum nigroviride, Lasioglossum pilosum, Lasioglossum planatum, Lasioglossum quebecense, Lasioglossum subviridatum, Lasioglossum truncatum, Lasioglossum versans, Lasioglossum versatum, Halictus confusus, Halictus rubicundus*
Green bees	93	48	141	*Agapostemon* *Augochlora* *Augochlorella* *Augochloropsis*	*Agapostemon sericeus, Agapostemon virescens, Augochlora pura, Augochlorella aurata, Augochloropsis metallica*

$$\frac{berry}{cane} \times \frac{cane}{bush} \times \frac{bush}{ha} = \frac{berry}{ha} \quad (1)$$

We then combine these yield estimates with our experimental results to estimate the yield losses resulting from pollen limitation. Following Gibbs et al. (2016), we defined yield deficit (Y_d) as the yield expected under full pollination (as estimated by hand treatments), minus yield under ambient pollination conditions (as estimated by open treatments):

$$Y_d = \left(\frac{berry}{ha} \times \left(\frac{FS_h}{FS_o}\right) \times M_h\right) - \left(\frac{berry}{ha} \times M_o\right) \quad (2)$$

where M_h and M_o are the average berry weight from hand- and open-pollinated treatments for each farm, respectively, and FS_h and FS_o are the average fruit set from hand- and open-pollinated treatments for each farm, respectively. We convert kilograms of berries into revenue by multiplying mass by the price reported by the 2015 NASS New England Fruits and Vegetables Report ($7.48/kg) (Keough, 2007).

3. Results

3.1. Pollen limitation in blueberry production

Pooling data across all farms, we found that blueberries are significantly pollen limited in this system (Fig. 1; Table A.1). Hand pollination increased seed set (significant in both years), fruit mass (both years) and fruit set (2014 only), indicating significant pollen limitation for variables related to blueberry production (Fig. 1A,B,C). Hand pollination also reduced variability in seed set (both years) and variability in fruit mass (2014 only), indicating pollen limitation in the uniformity of blueberry crops as well (Fig. 1D,E). Finally, hand pollination advanced harvest date for blueberries (2015 only), indicating that additional pollination would accelerate ripening times (Fig. 1F). These pooled results indicate overall study-wide effects, but obscure considerable variation in pollen limitation among farms (Fig. A.1). Understanding the role of wild pollinators in driving this variation is the main goal of this paper.

3.2. Bee visitation effects on harvest quantity and quality

In both years, blueberry production improved with increasing visitation by wild bees (Fig. 2; Table 2). Pollen limitation for seed set diminished exponentially as bee visitation increased (Fig. 2A; Table 2), and pollen limitation for fruit mass and fruit set diminished linearly as bee visitation increased (Fig. 2B,C; Table 2). In absolute terms, these changes corresponded to average improvements of 29 mature seeds (92% increase from study-wide mean for open treatment), 0.17 g of fruit mass (12% increase), and 9.6 percentage points in fruit set (12% increase).

Bee visitation also improved the uniformity of harvested blueberries and advanced the timing of harvest. Pollen limitation for the coefficient of variation (CV) of seed set diminished exponentially as bee visitation increased (Fig. 2D; Table 2), and pollen limitation for CV of fruit mass and date of 25% harvest diminished linearly as bee visitation increased (Fig. 2E,F; Table 2). These changes corresponded to improvements of 73% and 11% in uniformity of seed set and fruit mass, respectively, and an advancement of 2.5 days in ripening time.

Combining results for fruit mass and harvest time, we found a pollination effect on cumulative blueberry production over the summer (Fig. 3). In both years, the mass of harvested blueberries accumulated more rapidly for hand pollinated treatments, reaching 50% of total harvested mass two days earlier. At the end of the season, the total accumulated mass from hand pollinated treatments was 34% and 20% higher than from open treatments for 2014 and 2015, respectively (Fig. 3). The differences between treatments varied widely among farms (Fig. A.2), reflecting the variation among farms in pollen limitation (Fig. A.1).

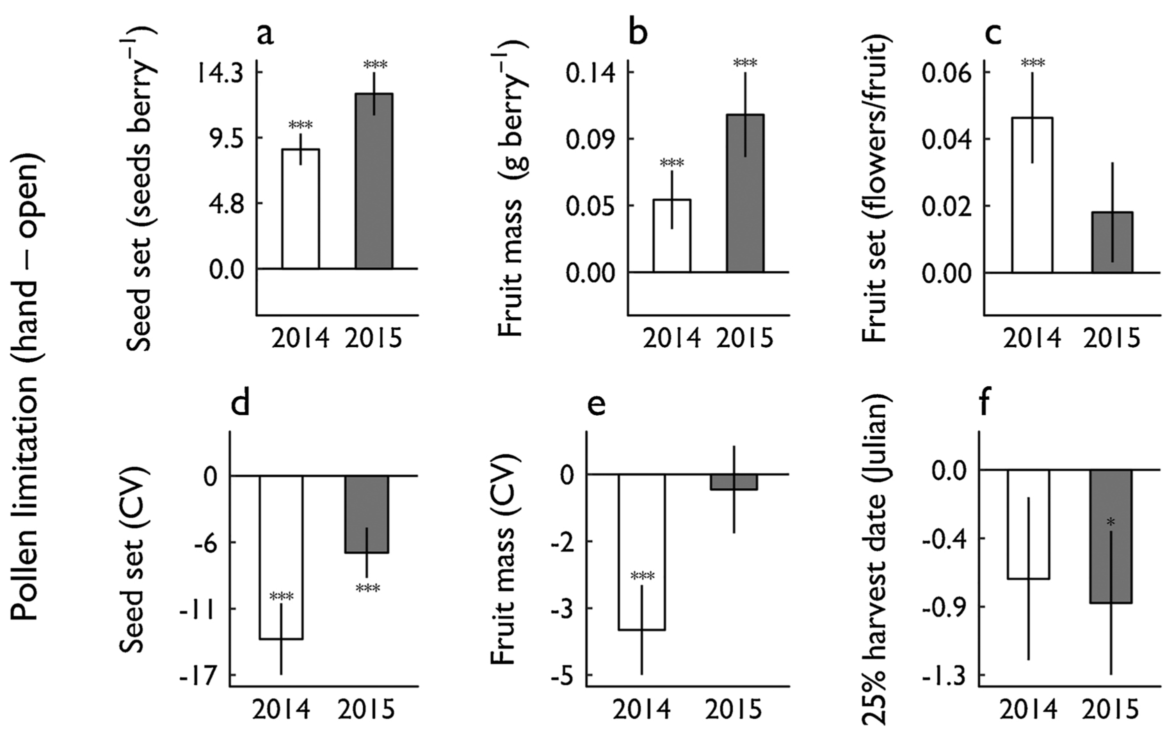

Fig. 1. Pollen limitation for blueberry production and quality. All bushes are pooled to estimate overall effects. Panels depict pollen limitation (i.e., hand pollination treatment – open treatment) for six key variables. A: Seed set; B: Fruit mass; C: Fruit set; D: coefficient of variation (CV) of seed set; E: coefficient of variation (CV) of fruit mass; F: date by which 25% of berries had been harvested. White bars: 2014; grey bars: 2015. Symbols represent results of 1-way t-tests, testing whether each mean = 0: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See Table A.1 for full statistical results.

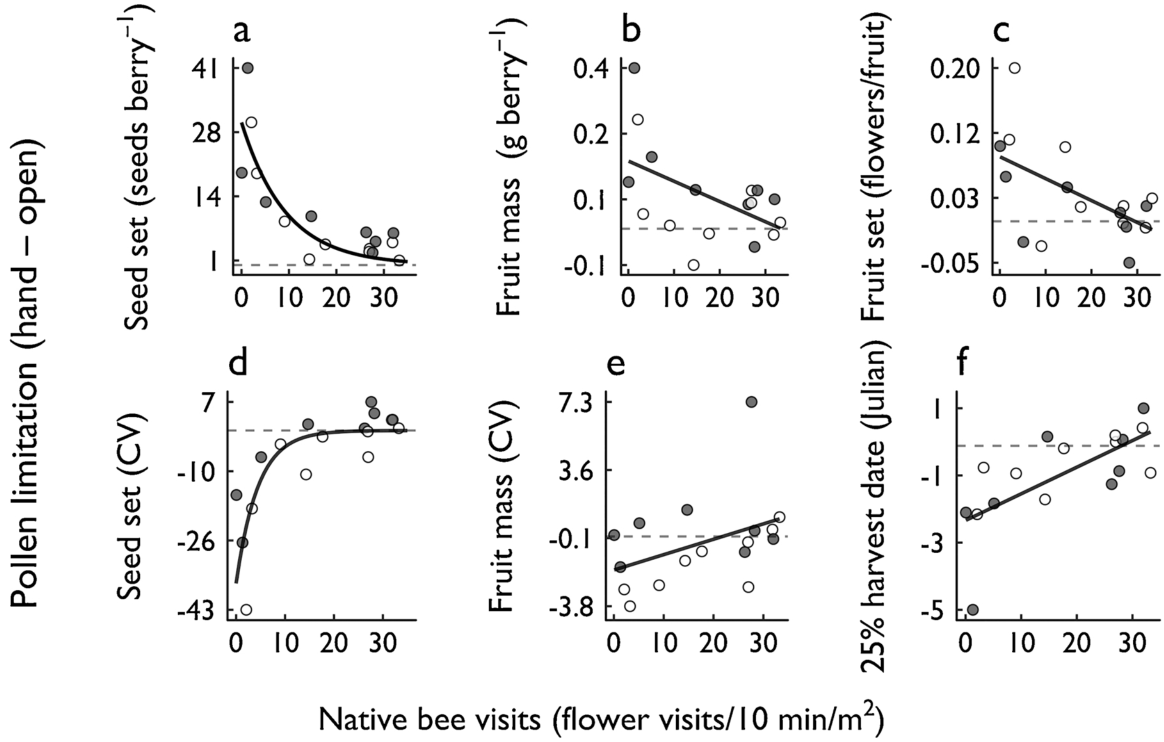

Fig. 2. Effects of wild bee visitation on pollen limitation for blueberry production and quality. Panels depict pollen limitation (i.e., hand pollination treatment – open treatment) for six key variables. A: Seed set; B: Fruit mass; C: Fruit set; D: coefficient of variation (CV) of seed set; E: coefficient of variation (CV) of fruit mass; F: date on which 25% of berries had been harvested. White symbols: 2014; grey symbols: 2015. Dashed horizontal lines indicate no pollen limitation, where open and hand treatments are equivalent. Curves are fit to pooled data from both years. All curves fit data significantly better than null models (Log-likelihood ratio tests); exponential curves are presented if they fit data significantly better than linear fits (Log-likelihood ratio tests). See Table 2 for statistical results.

Table 2
Statistical results of relationships between wild bee visitation and six measures of blueberry production and quality. Table reports log-likelihood tests between linear models and a null model, between exponential models and a null model, and between exponential and linear models. ΔAIC: difference in AIC (model minus null model or exponential model minus linear model); LLR: Log-likelihood ratio. P-values in bold are significant at 0.05 level. Variables for which exponential models have significantly better fits are represented with exponential curves in Fig. 2.

	Linear model			Exponential model			Exponential vs. linear model		
	ΔAIC	LLR	p-value	ΔAIC	LLR	p-value	ΔAIC	LLR	p-value
Seed set	−13.29	15.29	**0.0001**	−16.48	22.48	**0.0000**	−3.19	7.19	**0.0073**
Fruit mass	−3.36	5.36	**0.0206**	−2.75	8.75	**0.0031**	0.61	3.39	0.0657
Fruit set	−4.26	6.26	**0.0124**	−2.22	8.22	**0.0041**	2.04	1.96	0.1612
CV seed set	−12.82	14.82	**0.0001**	−16.42	22.42	**0.0000**	−3.60	7.60	**0.0058**
CV fruit mass	−2.23	4.23	**0.0397**	4.71	1.29	0.2565	6.94	−2.94	1.0000
25% harvest date	−9.02	11.02	**0.0009**	−7.39	13.39	**0.0003**	1.63	2.37	0.1239

3.3. *Differences among bee groups*

To compare the influence of visits by different morphospecies groups on pollen limitation, we fit exponential models for each group independently (analogous to Fig. 1A), using seed set as the response variable. We find that visitation rates by "*Bombus* (queen)" and "Black bees (big)" are most strongly related to reductions in pollen limitation (Fig. 4). "*Bombus* (worker)", "Black bees (slender)", and "Black bees (tiny)" also show significant negative exponential relationships. Visits by "Green bees" are not significantly related to pollen limitation.

3.4. *Economic costs of pollen limitation*

Farms also varied widely in the economic effects of pollen limitation on yield. Using Eq. (2) and results of field sampling (Table A.2), we estimate that pollen limitation reduced yield, and therefore revenue, between 1% (on Farm #6) and 36% (on Farm #9) (Fig. 5). Farms also varied widely in baseline yield (i.e., assuming open pollination treatment), due to differences in densities of bushes/ha, canes/bush, and berries/cane (Fig. A.3). At Farm #9, for example, high baseline yield combined with a large pollen limitation resulted in an expected loss of annual revenue of almost $137,000. We estimate more modest costs for other farms: from $461 on Farm #6 to $27,722 on Farm #3.

4. Discussion

Our findings indicate that wild pollinators are important to blueberry production, affecting both the quantity and quality of crops. Visits by wild bees lead to higher yields, more uniform berries, and faster ripening times. The magnitude of pollen limitation varies widely among farms, however, as does the economic benefit of alleviating it. Conserving wild pollinator communities within working landscapes can therefore improve bottom lines for farmers, but these improvements will benefit some farmers more than others.

By measuring six aspects of production, we gained insights into the range of pollination impacts on crops and farmers. Visits by wild bees

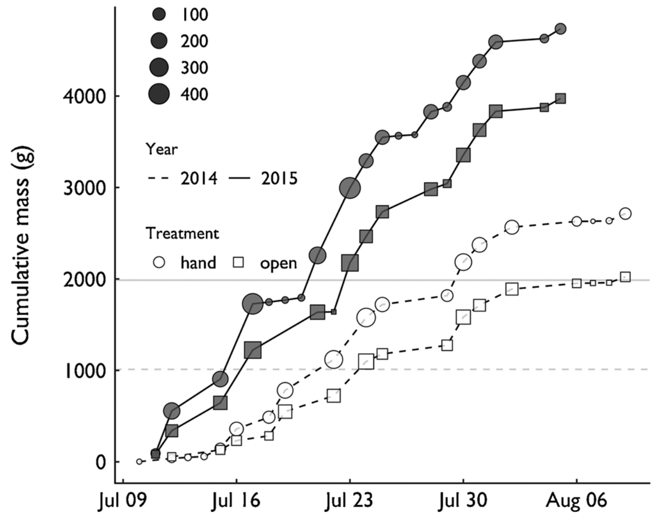

Fig. 3. Accumulated mass of harvested blueberries over two harvest seasons. Mass accumulates more rapidly for hand pollinated treatment in both years, and reaches 50% harvested mass two days earlier in both years. Open symbols and dashed lines: 2014; grey symbols and solid lines: 2015. Circles: hand pollinated treatment; triangles: open treatment. Symbol size corresponds to the number of blueberries harvested that day. Horizontal lines represent 50% of harvested mass in open treatment.

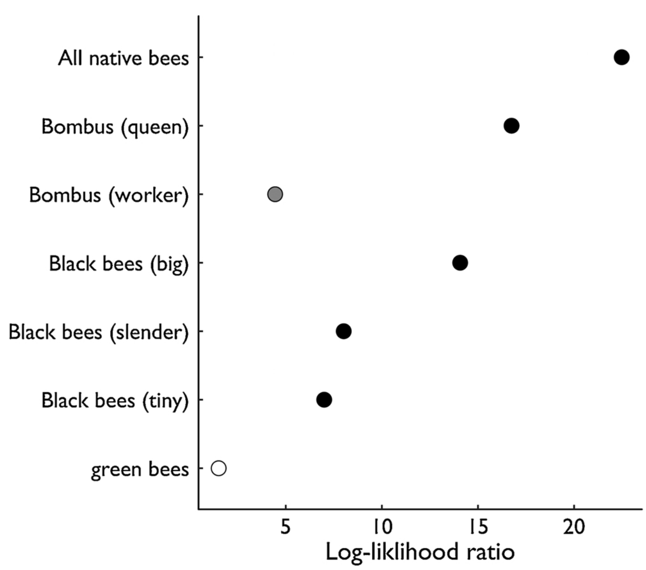

Fig. 4. Relationships between seed set and different bee groups. Symbols represent the fit of exponential models relating pollen limitation on seed set to visitation rate for each morphospecies group. Fit is measured with log-likelihood ratios comparing exponential and null models (see methods). These relationships and tests are equivalent to those depicted in Fig. 1A. Open symbols: ns; grey $p < 0.05$; black: $p < 0.01$.

dramatically reduced pollen limitation in seed set (Fig. 2), confirming that they are effective pollinators of blueberry flowers (Benjamin and Winfree, 2014; Button and Elle, 2014; Dogterom et al., 2000). The exponential shape of the relationship is what theory would predict for an ecological function with a saturating effect (Cardinale et al., 2012). Wild bee visits also relieved pollen limitation in two yield variables most relevant to growers: fruit mass and fruit set (Fig. 2). These relationships were weaker than that for seed set, likely because factors beyond pollination also contribute to berry number and size, such as water availability, soil fertility, and pruning. Although these two relationships were described best by linear functions, sample size may have limited our ability to detect a non-linear response.

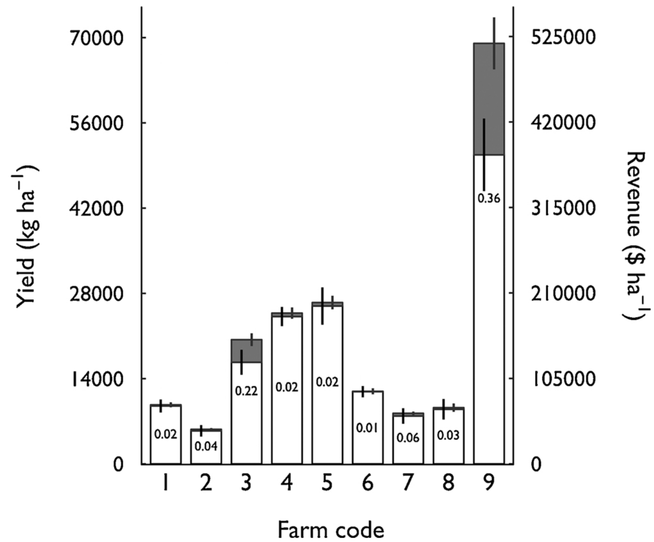

Fig. 5. Effects of pollen limitation on blueberry yield and revenue for each farm. Yield estimates combine fruit set and fruit mass effects using Eq. (2). White bars represent potential yield with ambient pollination (i.e., open pollination treatment). Grey bars represent added yield expected if pollen limitation is eliminated (i.e., hand pollinated treatment). The ratio of grey to white bars is the proportional increase expected (indicated by the number within each white bar). Error bars represent +- 1SD and are calculated independently for ambient and deficit portions of bars. White bars vary among farms due to differences in planting density, pruning, and other management factors (Fig. A.3). See Table A.2 for field estimates of all variables in Eq. (2). Farm codes correspond to those in Table A.2 and Figs. A.1–A.3.

Yield is not the only important aspect of production for blueberry growers. We found that visits by wild bees also improved fruit uniformity and ripening time. The relationship for uniformity of seed set was strong and exponential (Fig. 2), showing a clear and saturating biological response to pollination. Uniformity of fruit mass also improved with wild bee visits (Fig. 2), but showed a linear and weaker relationship. Berry uniformity can influence market price, with a premium placed on large and consistent berries (Gilbert et al., 2014). Visits by wild bees also advanced harvest by roughly 2 days for the most pollen limited farms (Fig. 2). Harvest timing can be important to growers to lengthen harvest season and reach markets earlier (Klatt et al., 2014). A difference of two days is unlikely to have a substantial economic effect in this case, but it is evidence that pollination affects more than yields.

Although visitation by most morphospecies groups significantly reduced pollen limitation (Fig. 4), visitation rates by two groups in particular showed the strongest effects. "*Bombus* (queens)" comprised 10 species of bumblebees, dominated by *B. impatiens* and *B. bimaculatus*. And "Black bees (big)" comprised several species of *Andrena* and *Osmia*, dominated by *A. carlini* and *A. vicina* (Table 1). These species were the most frequent visitors to blueberry flowers (Nicholson et al., 2017) and are known to be among the most effective at transferring pollen among them (Javorek et al., 2002). "*Bombus* (workers)" had a relatively weak effect (Fig. 4), likely because blueberries bloom in early spring, before queens have produced many workers. These group-wise results should be interpreted with caution, because visitation may be correlated among morphospecies. A stronger test would include each morphospecies in a multi-factor model (Garibaldi et al., 2013). We lacked sufficient site replication for this approach, but we observe generally weak correlations in visitation among morphospecies (Table A.3).

Another way to illuminate the relative importance of pollinator groups is to combine visitation rate with pollination effectiveness, often measured as the number of conspecific pollen grains deposited on a stigma per visit (Benjamin and Winfree, 2014; Cane and Schiffhauer, 2003; Javorek et al., 2002). We focus only on visitation rate in this study, but accounting for effectiveness is unlikely to change our results. The most common visitors in our system are also among the most effective pollinators. In fact, using per-visit deposition data from previous studies (Benjamin and Winfree, 2014; Javorek et al., 2002), we find that the order of morphospecies groups is unchanged when ranked by visitation rate or by pollination function (Fig. A.4).

The economic impact of pollen limitation on blueberry yields varied to a surprising degree among farms. Relieving pollen limitation would increase yields (kg of berries/ha) between 1–6% for most farms, but up to 22% and 36% for others (Fig. 5). This range indicates that in Vermont's relatively low intensity agricultural system, many farms already receive adequate pollination, but others have significant deficits and some are severe. While the yield increases themselves are driven in part by bee visitation, their resulting economic values are also determined by the density of flowers per ha, and thus potential yield under ambient pollination (i.e. white bars in Fig. 5).

In fact, in our system farms with higher potential yields (in particular farm #9) also tended to have high pollen limitation, leading to large economic values for relieving that limitation. This apparent paradox (Ghazoul, 2007; Klein et al., 2008) is actually an expected pattern: pollen limitation is likely to be greater on intensively managed farms, which often have both high flower densities and low pollinator abundance due to chemical pesticides and reduced bee habitat. Ghazoul (2007) argues that growers may have little economic incentive to support pollinators, because yields could instead be enhanced through intensifying management. However, the two strategies are not mutually exclusive; relieving pollen limitation can improve yields no matter the level of management intensity. Indeed, as farm #9 shows, relieving pollen limitation may have the highest payoff for intensively managed farms.

Fruit quality and harvest timing also likely affect demand and price (Gilbert et al., 2014; Saftner et al., 2008). The economic value of pollination on these attributes has been quantified in apples and strawberries (Garratt et al., 2014; Klatt et al., 2014). To our knowledge, data on specific price effects of these attributes are lacking in blueberry, which prevented similar analyses here. This is an area of future research.

While our results indicate the economic benefits of enhancing pollination (Fig. 5), any economic decision must compare benefits to costs. Restoring flower strips, nesting habitats, or hedgerows will bear establishment costs (e.g., soil preparation, seeding), maintenance costs (e.g., weeding, mowing), and opportunity costs (i.e., revenue that could have been earned from that same land). Estimating these costs for Vermont farms is beyond the scope of this study, but restoration costs in Michigan blueberry farms have been estimated at roughly $2400 over five years (Blaauw and Isaacs, 2014). For all but one of the Vermont farms studied here (farm #2), expected benefits of relieving pollen limitation for five years exceed these costs (Table A.2). Because both costs and benefits are likely to vary widely among farms, farm-specific studies and recommendations are needed to best inform decisions.

Our results build from those of Nicholson et al. (2017) to show the economic importance of managing agricultural landscapes to support wild pollinators. In this same system, Nicholson et al. (2017) found that pollinator visitation increased with increased natural land cover surrounding farms, reduced intensity of farm management, and the interaction between these factors. Here we show that these increased pollinator visits can improve the quantity and quality of crops and can increase revenues. Beyond this particular system, other studies indicate that pollinators respond to landscape composition and farm-level management (Garibaldi et al., 2011; Kennedy et al., 2013; Klein et al., 2012; Park et al., 2015; Ricketts et al., 2008) and that bee visitation reduces pollen limitation and improves crop yields (Benjamin and Winfree, 2014; Button and Elle, 2014; Cusser et al., 2016; Garibaldi et al., 2013). Actions to support wild pollinators at both landscape and local scales, therefore, can improve economic returns for farmers and enhance biodiversity.

Our study extends this growing literature in three important ways. First, by harvesting every berry as it ripened, we were able to compliment estimates of production with measures of crop quality such as berry uniformity and ripening time. This harvesting approach also allowed us to estimate realized production, instead of proxy measures from sampled berry clusters of mixed maturity (Blaauw and Isaacs, 2014; Button and Elle, 2014; Gibbs et al., 2016). Second, we investigate these relationships in a system that is not dominated by honeybees, as so many others are (Button and Elle, 2014; Cusser et al., 2016; Gibbs et al., 2016; Kremen et al., 2002). This allows us to understand ecosystem services provided by wild populations of native bees, without augmentation by honeybees (Fig. 2). Finally, as mentioned above, we focus on a low intensity agricultural system. Pollination services are relatively understudied in these systems, despite their prevalence worldwide and dominance in many regions (Fritz et al., 2015; Lowder et al., 2016). Even in complex landscapes with seemingly abundant resources for bees, we find that habitat conservation and pollinator management can improve pollination and resulting yields.

More generally, our findings illustrate the importance of wild pollinators to both the quantity and quality of crops. Maintaining pollinator populations in agricultural landscapes can therefore benefit farm economies, food systems, and native species alike.

Authors' contributions

Both authors contributed equally to this work. TR designed the study, CN and TR collected the data; CN analyzed the data, TR and CN wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

Data availability

Data available from figshare digital repository: https://figshare.com/projects/2019_Nicholson_Blueberry_Yield/55469.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.10.018.

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