

Does Passive Sampling Accurately Reflect the Bee (Apoidea: Anthophila) Communities Pollinating Apple and Sour Cherry Orchards?

Jason Gibbs,^{1,2,3} Neelendra K. Joshi,^{4,5} Julianna K. Wilson,¹ Nikki L. Rothwell,⁶ Karen Powers,⁶ Mike Haas,¹ Larry Gut,¹ David J. Biddinger,⁴ and Rufus Isaacs¹

¹Department of Entomology, Michigan State University, 570 Wilson Rd., East Lansing, MI 48824 (jason.gibbs@umanitoba.ca; jk wilson@msu.edu; haasm@msu.edu; gut@msu.edu; isaacs@msu.edu), ²Current Address: Department of Entomology, University of Manitoba, 12 Dafoe Rd., Winnipeg, Manitoba, R3T 2N2, Canada, ³Corresponding author, e-mail: jason.gibbs@umanitoba.ca, ⁴Department of Entomology, Penn State University, 501 ASI Bldg., University Park, Pennsylvania, PA 16802 (nkjoshi@uark.edu; djb134@psu.edu), ⁵Department of Entomology, University of Arkansas, 319 Agricultural Bldg., Fayetteville, Arkansas, 72701, and ⁶Northwest Michigan Horticultural Research Center, Michigan State University, 6686 S. Center Highway, Traverse City, Michigan, 49684 (rothwel3@msu.edu; zingerk@msu.edu)

Subject Editor: Theresa Pitts-Singer

Received 13 November 2016; Editorial decision 8 March 2017

Abstract

During bloom of spring orchard crops, bees are the primary providers of pollination service. Monitoring these insects for research projects is often done by timed observations or by direct aerial netting, but there has been increasing interest in blue vane traps as an efficient passive approach to collecting bees. Over multiple spring seasons in Michigan and Pennsylvania, orchards were monitored for wild bees using timed netting from crop flowers and blue vane traps. This revealed a distinctly different community of wild bees captured using the two methods, suggesting that blue vane traps can complement but cannot replace direct aerial netting. The bee community in blue vane traps was generally composed of nonpollinating species, which can be of interest for broader biodiversity studies. In particular, blue vane traps caught *Eucera atriventris* (Smith), *Eucera hamata* (Bradley), *Bombus fervidus* (F.), and *Agapostemon virescens* (F.) that were never collected from the orchard crop flowers during the study period. Captures of bee species in nets was generally stable across the 3 yr, whereas we observed significant declines in the abundance of *Lasioglossum pilosum* (Smith) and *Eucera* spp. trapped using blue vane traps during the project, suggesting local overtrapping of reproductive individuals. We conclude that blue vane traps are a useful tool for expanding insights into bee communities within orchard crop systems, but they should be used with great caution to avoid local extirpation of these important insects.

Key words: agriculture, pollinator, sampling, tart cherry, tree fruit

Bees (Apoidea: Anthophila) are the predominant pollinators of agricultural crops and wildflowers (Ollerton et al. 2011). Although a diverse community of wild bees may be important for reliable crop pollination service (Winfree and Kremen 2009, Bartomeus et al. 2013), it is evident that most flower visits to crop plants are by the most dominant bee species (Kleijn et al. 2015, Winfree et al. 2015). In large commercial fields and orchards in simplified landscapes where wild bee abundance is limited, managed honey bees, *Apis mellifera* L., can be the primary predictor of pollination (Allsopp et al. 2008, Isaacs and Kirk 2010, Gibbs et al. 2016), whereas in other agro-ecosystems with more complex landscapes, wild bees are also extremely important for crop pollination (Winfree et al. 2008, Garibaldi et al. 2013, Mallinger and Gratton 2015, Blitzer et al. 2016, Park et al. 2016). In some diverse cropping systems where field sizes are small or natural habitat is available, wild bees may be

capable of supplying the majority of crop pollination requirements (Winfree et al. 2008, Isaacs and Kirk 2010).

Apple (*Malus pumila* Mill.; Rosaceae) and sour cherry (*Prunus cerasus* L.; Rosaceae) are pollinator-dependent crops that bloom in the early spring (Free 1993, Delaplane and Mayer 2000, Garratt et al. 2014). Pollinator communities of apple have been well-studied both historically and in recent years (Atwood 1933, Boyle and Philogene 1983, Watson et al. 2011, Mallinger and Gratton 2015, Russo et al. 2015, Blitzer et al. 2016). Despite these efforts, a full understanding of the pollinator community is challenging to document owing to temporal and spatial variation (Russo et al. 2015). Most research on sour cherry pollinators has focused on *A. mellifera* (McGregor 1976); less is known about its wild pollinators (but see Hansted et al. 2015). Based on the common spring bloom time and similar floral morphology, the pollinator communities of apple and

sour cherry are expected to be similar. However, sour cherry blooms 1–2 wk before apple, at a time when weather conditions are often not suitable for bee flight. Inconsistent weather in early spring causes large interyear variation in bloom phenology and duration that make sampling for bees and pollination difficult in these crops.

Pollinator communities in apple orchards have been documented using a combination of sampling techniques, such as aerial nets, colored cups, bowls, and vane traps (Russo et al. 2013, Joshi et al. 2015, Kleijn et al. 2015, Mallinger and Gratton 2015, Garratt et al. 2016). Although active netting of bees from flowers is a direct measure of floral visitation, the number of sampling opportunities are limited by the short bloom time of spring tree fruit crops and frequent periods of poor weather within the bloom period. Passive sampling is attractive as a means of sampling many sites simultaneously with lower labor needs and the added benefit of collecting bees during short and often unpredictable breaks in the weather that are favorable for bees. Blue vane traps (BVTs) have recently been shown to be more effective at capturing a diversity of bees in this system than other passive sampling methods (Joshi et al. 2015). Earlier studies show that BVTs collect an abundance of large-bodied apid bees, such as bumble bees (*Bombus* spp.) and *Eucera* spp., (Stephen and Rao 2005, Rao et al. 2009, Kimoto et al. 2012, Geroff et al. 2014, Joshi et al. 2015, Mogren et al. 2016), that are less commonly captured in bowl traps (Droege et al. 2010, Geroff et al. 2014, Joshi et al. 2015). Blue vane traps have been suggested as a complementary sampling method to include in research and monitoring programs for a more complete picture of the bee fauna (Stephen and Rao 2007, Joshi et al. 2015), but comparative trapping studies show that some species may be missed by BVTs (Geroff et al. 2014, Joshi et al. 2015). Spring sampling using BVTs have revealed relatively few andrenid bees (Joshi et al. 2015) in comparison with studies in similar habitats using net collections (Watson et al. 2011, Martins et al. 2015, Russo et al. 2015), but studies have not compared BVT captures to net samples directly. One potential downside of BVTs is that they may capture large numbers of bees that are unlikely to be associated with the crop under investigation (Joshi et al. 2015, Mogren et al. 2016). Additionally, there is concern that a propensity to capture foundress bees of social species during the early spring period could negatively affect bee populations (Gezon et al. 2015). Solitary species provision cells sequentially without further parental care after cell completion, so reproductive investment in subsequent generations prior to capture is not lost when a female is trapped. In contrast, social species that begin to nest in early spring during sour cherry and apple bloom are unlikely to be at a stage where reproductive offspring are being produced. If BVTs are highly efficient, capturing foundress females could lead to a local extirpation of these species.

To improve understanding of tree fruit pollinator communities in eastern U.S. orchards, and to address the opportunities and concerns regarding BVTs, we compared wild bee communities monitored in Michigan and Pennsylvania apple and sour cherry orchards collected using direct aerial netting from crop flowers and BVTs. We specifically asked whether the bee communities were different between the two monitoring methods, whether the temporal and spatial patterns of captures varied using these methods, and whether particular bee species were affected by the use of these sampling methods.

Materials and Methods

Study Systems

We sampled nine sour cherry orchards from 2014 to 2016 across major growing regions in Van Buren, Berrien, Oceana, and

Leelanau Counties in the western region of Michigan's Lower Peninsula. These four counties represent three major growing regions in the southwest (Berrien and Van Buren), central (Oceana), and northwest (Leelanau) of the Lower Peninsula. Michigan is the primary producer of sour cherry in the United States, and all orchards were at least 1 km apart, at least 2 ha, and located next to a woodlot in a heterogeneous landscape that included other orchards and crop fields as well as natural wooded habitat. Soils are sandy in the western region of Michigan where sour cherry is grown. In addition, six commercial apple and four sour cherry orchards in Adams County, PA, were sampled from 2012 to 2014 and in 2015, respectively. For more details on Pennsylvania apple orchards see Joshi et al. (2015, 2016). All apple and cherry orchards in Pennsylvania were located in Adams County, which is the major fruit-growing region of the state. Similar to Michigan, these orchards were adjacent to natural habitats comprising diverse landscapes, and were at least 1.6 km apart. Most apple orchards were 5–8 km apart and cherry orchards were within ~3–5 km from one another, with one cherry orchard separated by 40 km.

Collection Methods

In Michigan, transects were set up at the orchard border and at 25, 50, and 100 m into the orchard in a study design similar to that described in Gibbs et al. (2016). Bees were actively netted for a combined 30 min. per transect by multiple collectors during peak bloom. Collectors were of varying experience levels, ranging from undergraduate technicians to professional bee biologists. Inexperienced collectors are likely to be biased toward large-bodied species. Owing to the short bloom duration of sour cherry, only a single collection day was possible per field in each year. A BVT (SpringStar Inc., Woodinville, WA) was hung in the canopy at each distance at the start of bloom and left for 7–10 d. As a result, BVTs collected bees both during and after crop bloom.

In Pennsylvania, net collections were made in five zones defined by range of distances (0–15 m, 16–35 m, 36–55 m, 56–100 m, and 101–200 m) measured from the orchard edge rather than as transects at set distances as described above. These ranges were used because orchards in the hilly Pennsylvania landscape are less regularly shaped than Michigan ones, making straight transects at set distance impractical. Blue vane traps were placed at 15, 35, 55, 100, and 200 m from the orchard border and used to collect bees for the entire flight season of wild bees from April to September. To better match the sampling in Michigan, we only used Pennsylvania collection dates within a week of net collections to limit the captures to individual bees potentially foraging on crop blooms. Collected bees were returned to laboratories at Michigan State University and Penn State University, to be processed and labeled for later identification.

Identifications

All Michigan material was identified by J.G. Pennsylvania specimens were identified by a combination of D.B., Robert Jean (Environmental Solutions & Innovations, Inc., Cincinnati, OH), Sam Droege (USGS Patuxent Wildlife Research Center, Beltsville, MD), and J.G. Bees were identified using published revisions (Mitchell 1960, 1962; LaBerge and Bouseman 1970; LaBerge 1971, 1973, 1977, 1980, 1987, 1989; LaBerge and Ribble 1975; Bouseman and LaBerge 1979; Laverty and Harder 1988; Michener et al. 1994; Michener 2000; McGinley 2003; Gibbs 2011; Rehan and Sheffield 2011; Gibbs et al. 2013), online keys available at <http://www.discoverlife.org/mp/20q?search=Apoidea> (Andrus and Droege 2016a,b; Droege 2016; Droege and Rehan 2016;

Droege and Tucker 2016; Griswold et al. 2016; Larkin et al. 2016) and reference material in the A. J. Cook Arthropod Research Collection (Michigan State University). All specimens are vouchered at Michigan State University or at Penn State University in the Frost Entomological Museum, State College, PA, or the Fruit Research and Extension Center, Biglerville, PA.

Analyses

All statistical analyses were performed using R version 3.2.2 (R Core Team 2015). The *vegan* package (Oksanen et al. 2013) was used for community analyses. We used nonmetric multidimensional scaling ordination using the Morisita–Horn distance to compare bee communities across sites. We used permutational multivariate analysis of variance (PERMANOVA) to test for effects of year, collection method, crop, and study region on bee communities. Owing to typical nonnormality in the bee count data, nonparametric Kruskal–Wallis tests with post hoc Dunn’s tests or Wilcoxon (W) signed rank tests were used to compare collection methods.

We assessed the most abundant bees collected using the two collection methods in two ways. The first was the minimum number of species required to account for 80% of total collections. This cut-off was based on the relationship of the rank abundance order of species and cumulative flower visits from Kleijn et al. (2015). The second method used the inflection point of the rank abundance curve calculated using the R package *inflection* (Christopoulos 2012, 2016), grouping species to the left of the inflection point as dominant species (Supp. Fig. 1 [online only]). The percent of total collections using the inflection point ranged from 56 to 85% ($\bar{X} = 71\%$).

Results

In Michigan sour cherry orchards, we collected a total of 4,434 individual bees from 2014 to 2016—2,536 using BVTs and 1,898 from crop flowers using aerial nets (Supp. Table 1 [online only]). No significant difference was found between BVTs and nets for bee abundance ($W = 181$, $P = 0.86$), species richness ($W = 139.5$, $P = 0.24$), Chao-1 estimated richness ($W = 166$, $P = 0.59$), or the Shannon–Wiener diversity index ($W = 154$, $P = 0.41$). Comparing across years (2014–2016), we found no significant differences in these four metrics for net collections (Fig. 1A). However, when comparing the catches of bees in BVTs, there was a significant reduction in the abundance of bees captured compared with the previous year (Dunn’s test with Bonferroni correction, $P < 0.001$). Species richness followed a similar pattern (Dunn’s test with Bonferroni correction, $P < 0.001$; Fig. 1B).

In Pennsylvania sour cherry orchards, we collected 875 individual bees in 2015—767 using BVTs and 108 from crop flowers using nets (Supp. Table 2 [online only]). Despite the large differences in collections, using each orchard as a replicate, no significant difference was found between BVTs and nets for bee abundance ($W = 10$, $P = 0.13$), species richness ($W = 10$, $P = 0.13$), Chao-1 estimated richness ($W = 10$, $P = 0.13$), or the Shannon–Wiener diversity index ($W = 6$, $P = 0.88$).

In Pennsylvania apple orchards, we collected 550 individual bees between 2012 and 2014—420 using BVTs and 110 with nets (Supp. Table 3 [online only]). We found significantly greater bee abundance ($W = 74$, $P < 0.01$), observed species richness ($W = 77$, $P < 0.01$), Chao-1 estimated richness ($W = 69$, $P = 0.02$), and Shannon–Wiener diversity ($W = 76$, $P < 0.01$) in BVTs. Comparing across years (2012–2014), there were no significant differences in the four metrics of bee communities for net collections (Fig. 1C). However, BVT

collections in 2012 had significantly lower abundance (Dunn’s test with Bonferroni correction, $P < 0.01$) and richness (Dunn’s test with Bonferroni correction, $P < 0.05$) of wild bees compared with the following year (Fig. 1D).

When bee communities were compared using nonmetric multidimensional scaling, we found strong clustering of the two regions (MI vs. PA) and collection methods (nets vs. BVTs; Fig. 2). Results of the PERMANOVA analysis found that composition of the bee community was significantly affected by the crop type ($F = 3.20$, $df = 1$, $P = 0.002$), collection method ($F = 9.99$, $df = 1$, $P = 0.001$), region ($F = 3.25$, $df = 1$, $P = 0.001$), and collection year ($F = 3.78$, $df = 4$, $P = 0.001$; Table 1). To avoid confounding aspects of year, crop, and region, we also analyzed the two regional data sets separately (Figs. 3 and 4). In Michigan, significant effects of collection method ($F = 9.39$, $df = 1$, $P = 0.001$), year ($F = 2.67$, $df = 2$, $P = 0.001$), and geography (among the three major growing areas; $F = 1.39$, $df = 2$, $P = 0.001$), remained (Table 2). In Pennsylvania apple orchards, collection method significantly affected the bee communities trapped ($F = 7.85$, $df = 1$, $P = 0.001$), but the year of sample did not ($F = 1.45$, $df = 2$, $P = 0.08$; Table 3).

We compared the species composition collected from each crop, region, and method combination, for the bees that composed 80% of the total collections (Supp. Figs. 2–7 [online only]). Of the 73 species collected using nets in Michigan sour cherry orchards, the distribution was dominated by 13 species, 9 of which were in the genus *Andrena* (Andrenidae), where *Andrena miserabilis* Cresson was the most abundant species overall. Of the 80 species collected using BVTs in these same orchards, *Lasioglossum pilosum* (Smith) (Halictidae) surpassed all other species in terms of abundance in BVTs, comprising 45% of all bees collected using this method (1,134 out of 2,356 total). However, this species showed a dramatic reduction in abundance after the first year, with captures declining by >98%, from 1,082 females in 2014, to 18 and 34 females in 2015 and 2016, respectively. Eight additional species made up the top 80% of individuals in BVT collections, including five other halictid bees, *Bombus fervidus* (F.) (Apidae), *Eucera atriventris* (Smith) (Apidae), and *Andrena carlini* Cockerell. All *Bombus*, halictid bees, and *An. carlini* in BVTs were females, but *Eucera* collections were predominately male. *Andrena carlini* was the 14th most abundant species in nets, and *B. fervidus* and *E. atriventris* were never collected from crop flowers, nor was the second most abundant species, *Agapostemon virescens* (F.) (Halictidae). Similar to *L. pilosum*, collections of *Eucera* spp., declined dramatically in subsequent years from 130 individuals to 0 (Fig. 5). The number of *Bombus* collected went from 132 in 2014, to 11 and then 22 in the next 2 yr. *Lasioglossum pilosum* was the only species in common between the top 80% of collections from nets and BVTs.

Similar patterns were found in Pennsylvania sour cherry orchards. Eleven bee species comprised the top 80% of net collections, including nine species of *Andrena*. In this case, *Andrena nasonii* Robertson was the most abundant species collected. *Xylocopa virginica* (L.) and *Bombus impatiens* Cresson were also among the top pollinators collected from crop flowers. In contrast, only five species were required to make up 80% of BVT captures. Four of these species were never seen in net collections, and similar to the Michigan data they include *B. fervidus*, *L. pilosum*, and a *Eucera* species. *Eucera hamata* (Bradley) comprised nearly two-thirds (66%) of all collections from BVTs in Pennsylvania sour cherry orchards, despite being absent in the netting samples.

In Pennsylvania apple orchards, the distinction between net and BVT samples was less pronounced than in Michigan. Five species were shared among the top 80% of collections using these two

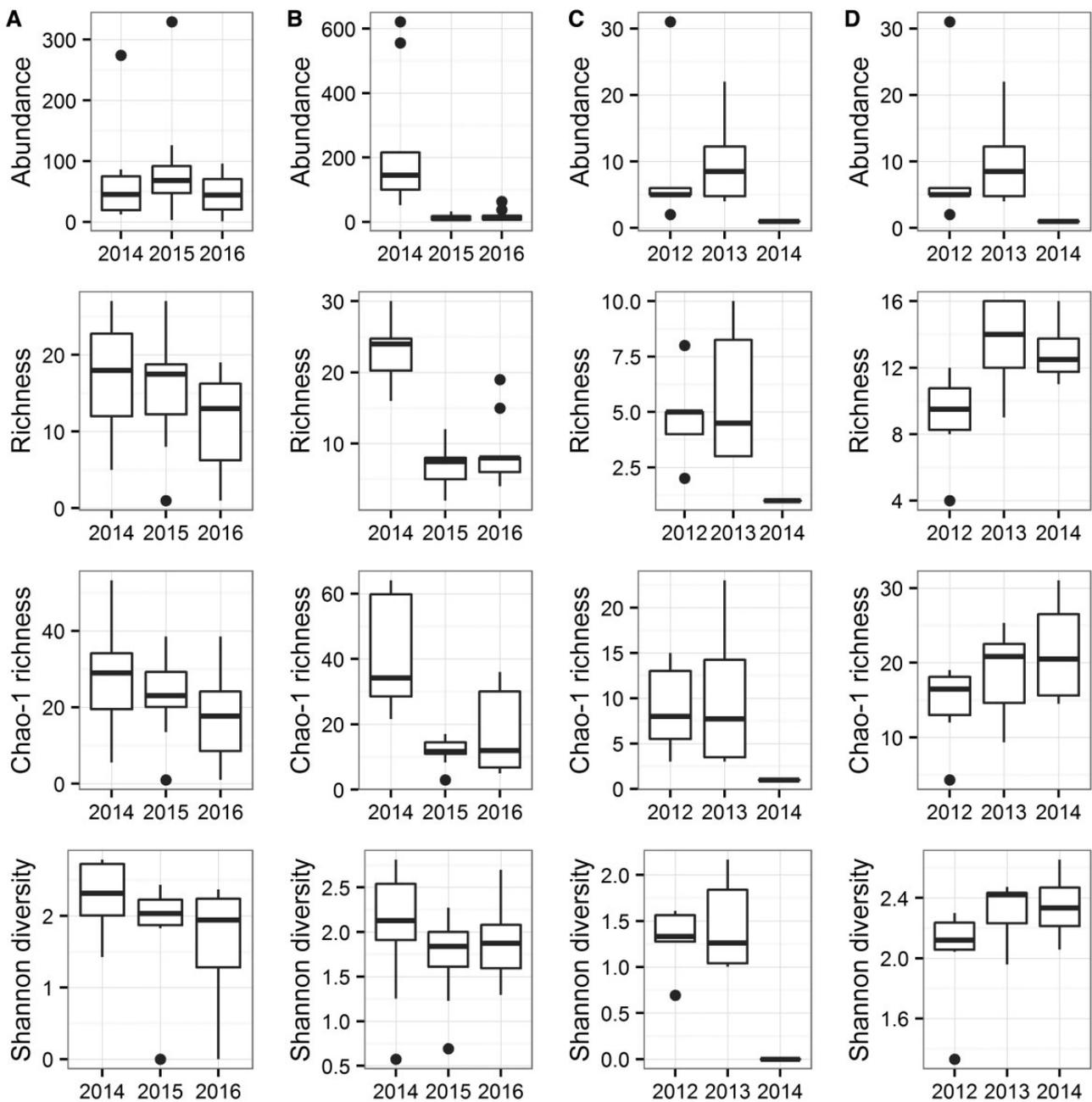


Fig. 1. Bee abundance, species richness, Chao-1 estimated species richness, and Shannon–Wiener diversity based on samples from (A) aerial nets in Michigan sour cherry orchards, (B) blue vane traps in Michigan sour cherry orchards, (C) aerial nets in Pennsylvania apple orchards, and (D) blue vane traps in Pennsylvania apple orchards.

methods. However, we again found that *B. fervidus* and *E. hamata* were abundant in BVTs, first and second most common respectively, whereas neither species was ever collected from flowers using nets. Four other species were found to be abundant in BVTs but were not captured from flowers, including the *Viola*-specialist *Andrena violae* Robertson. No single species was dramatically more abundant than other species in BVTs in this system, and 12 species in total were required to make the top 80% of collections. In net collections, nine species were required to make up the top 80%, including two species of *Bombus* and multiple *Andrena* species. The positions for eighth and ninth most abundant species were a six-way tie among species of equal abundance.

To determine if BVTs are effective proxies for net collections in spite of the differences in species identity and relative abundance observed, we tested for correlations between the two collection methods in bee abundance, richness, Chao-1 estimated richness, and Shannon–Wiener diversity (Fig. 6). No significant correlations were found, although the Chao-1 richness was marginally significant (Spearman’s correlation, $S = 9410$, $P < 0.06$). We used Michigan data to test if BVTs were capturing disproportionately higher numbers of the common bees at orchard borders owing to increased visibility of traps (Fig. 7; Supp. Fig. 8 [online only]). We found no significant effect of distance on abundance of the top nine species in Michigan BVTs (Kruskal–Wallis: $\chi^2 = 0.47$, $df = 3$, $P = 0.92$).

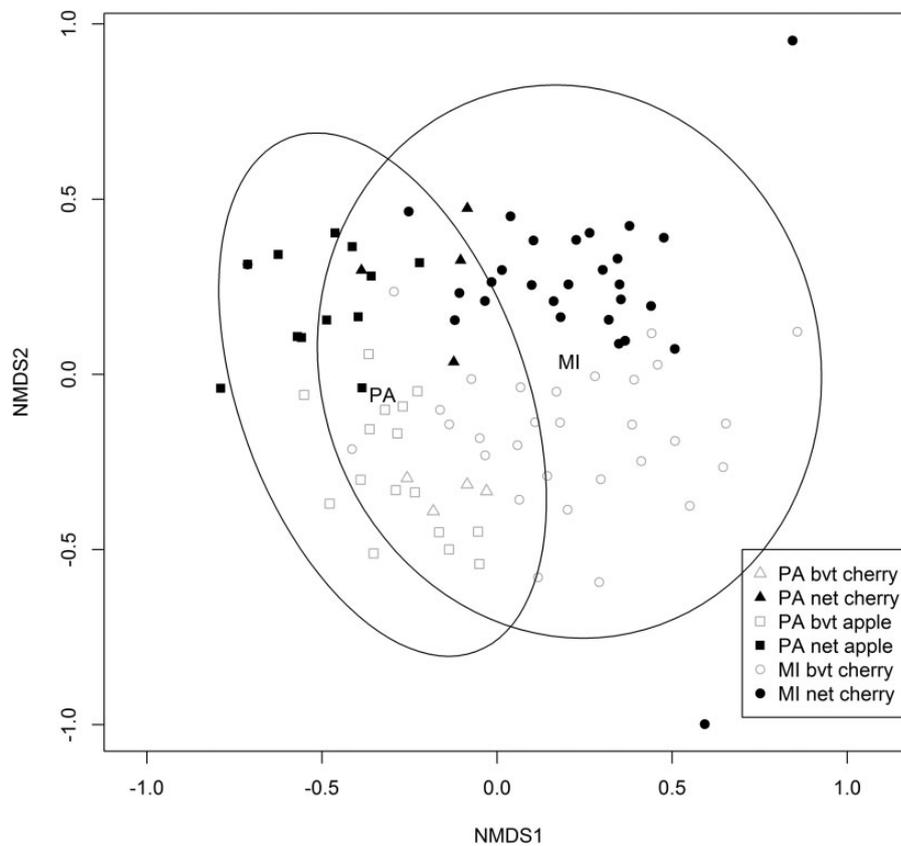


Fig. 2. Nonmetric multidimensional scaling ordination plot using the Morisita–Horn index of bee communities in apple and sour cherry orchards sampled with blue vane traps (bvt) and aerial nets from crop flowers (net) collected in Pennsylvania (PA) and Michigan (MI).

Table 1. Results of PERMANOVA using Morisita–Horn distances across all samples

	d.f.	Sums of sqs	Mean Sq	F.Model	R ²	Pr(>F)
Method	1	3.17	3.17	9.99	0.086	0.001
Year	4	4.80	1.20	3.78	0.13	0.001
Crop	1	1.03	1.03	3.25	0.03	0.001
State	1	1.02	1.02	3.20	0.03	0.002
Residuals	85	26.99	0.32	0.73		

Discussion

Our results demonstrate that despite the effectiveness of BVTs at capturing wild bees, the composition of the bee community is dramatically different than the species that visit orchard crop flowers. *Bombus fervidus* and members of the genus *Eucera* were common in BVTs in all three of our study systems, which may be interpreted as indicating that they are important pollinators of tree fruit in our region. However, these bees were never associated directly with crop flowers. *Eucera atriventris* and *E. hamata* have been collected from numerous plant species, but they are most often associated with members of the families Fabaceae and Plantaginaceae, visiting genera such as *Astragalus*, *Lathyrus*, *Trifolium*, *Vicia*, and *Penstemon* (Timberlake 1969). Similar floral preferences are true of *B. fervidus*, although it is more polylectic (Williams et al. 2014). Bumble bees are known to partition floral resources based on tongue-length and corolla depth (Heinrich 1976). Apple and cherry both have short-corolla flowers, and net collections of bumble bees were mostly short to medium-tongued, whereas BVTs captured primarily

long-tongued bumble bees such as *B. fervidus* (Medler 1962, Kearns and Thomson 2001; Supp. Fig. 9 [online only]). Although classification of bumble bee tongue lengths into discrete categories can vary among researchers, particularly for intermediate lengths (Kearns and Thomson 2001, Williams et al. 2014), the two abundant species captured only in BVTs, *Bombus borealis* Kirby and *B. fervidus*, are invariably considered long-tongued (Medler 1962, Kearns and Thomson 2001, Williams et al. 2014). Both *Eucera* spp. and *B. fervidus* are large-bodied species that fly during hours when net collections were made (J.G. personal observation), as such it seems improbable that such abundant species would have been missed entirely had they been visiting the crop flowers, as even relatively inexperienced collectors are likely to be biased in favor of collecting such conspicuous species. We expect that the light reflectance characteristics of BVTs (see Joshi et al. 2015), mimics that of preferred host plants of these bees, potentially acting as a supernormal stimulus (Dawkins and Krebs 1979, Gwynne and Rentz 1983) and leading to their attraction to, and capture by, these traps.

Similarly biased captures by BVTs have been reported in other crop studies. Stephen et al. (2009) report *Bombus californicus* Smith as the dominant species captured by BVTs in Oregon blueberry fields (49% of total), although they were rarely observed on crop flowers (4% of total). *Agapostemon virescens*, an extremely abundant species in BVTs placed in Michigan cherry orchards, but not in net captures, was also found in unusually high abundance in Oregon sunflower plots, representing 50.8% of all BVT captures and only 5.4% of sweep net samples (Stephen and Rao 2007). A recent survey of potato field pollinators using BVTs found a high proportion of apid bee captures (44%) to be *Peponapis pruinosa* (Say)

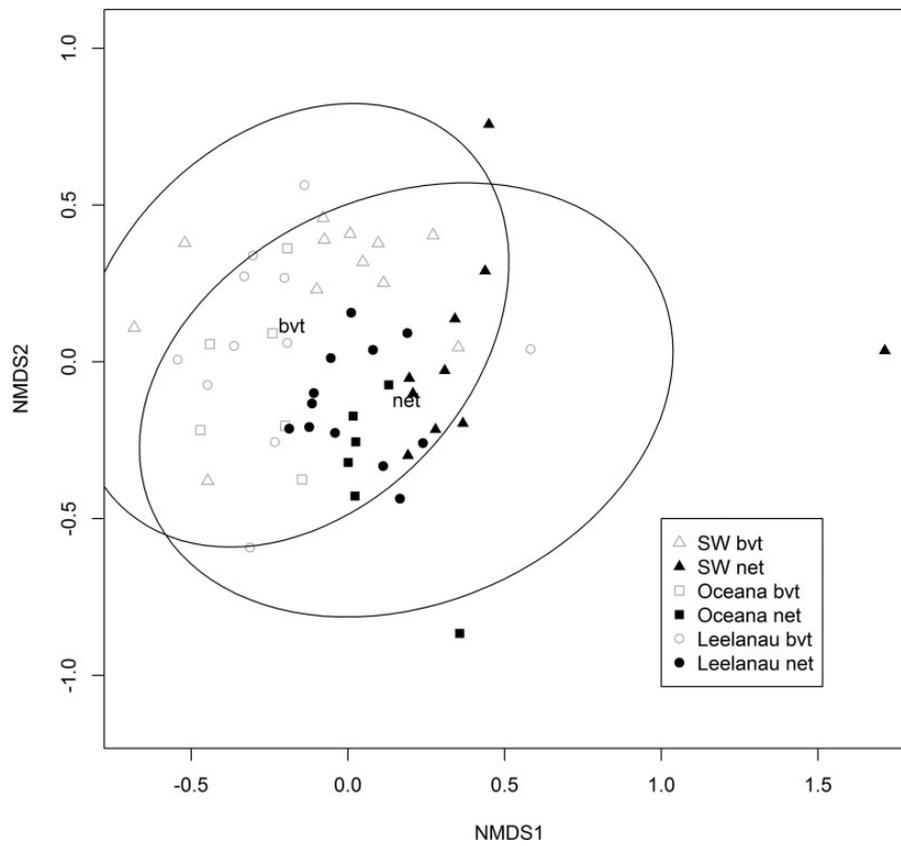


Fig. 3. Nonmetric multidimensional scaling ordination plot using the Morisita–Horn index of bee communities in Michigan sour cherry orchards sampled with blue vane traps (bvt) and aerial nets from crop flowers (net) collected in Lower Peninsula counties from the southwest (SW; Berrien and Van Buren), west central (Oceana), and northwest (Leelanau).

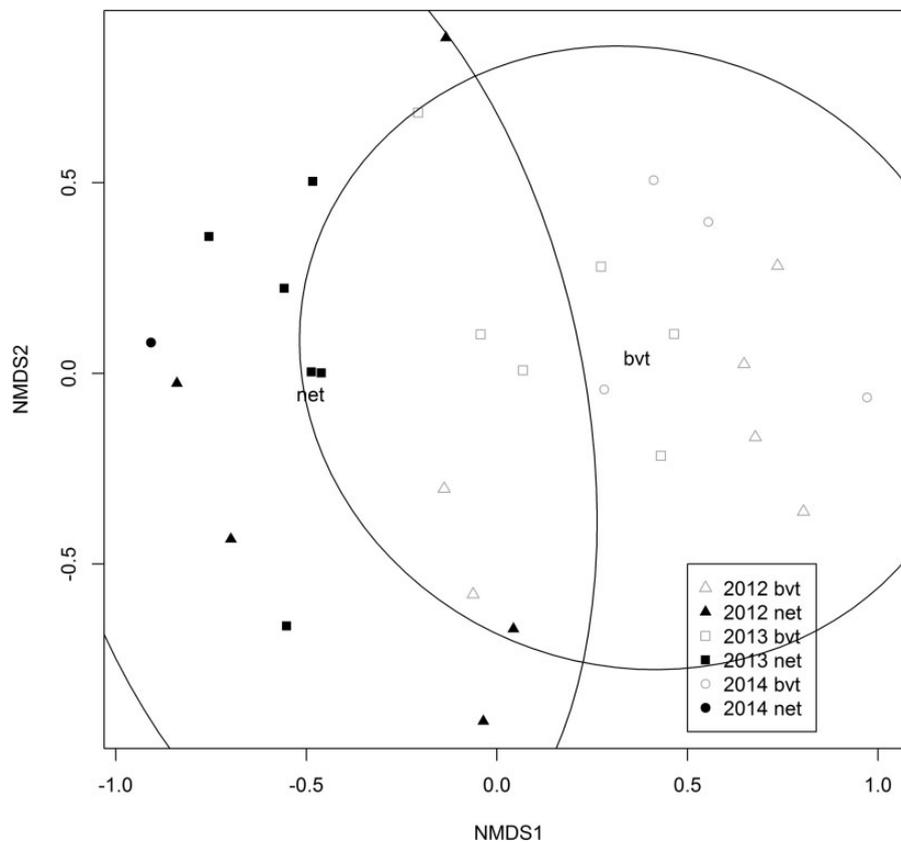


Fig. 4. Nonmetric multidimensional scaling ordination plot using the Morisita–Horn index of bee communities in Pennsylvania apple orchards sampled with blue vane traps (bvt) and aerial nets from crop flowers (net) collected Adams County from 2012 to 2014.

Table 2. Results of PERMANOVA using Morisita–Horn distances across Michigan sour cherry orchards (2014–2016)

	d.f.	Sums of sqs	Mean sqs	F.Model	R ²	Pr(>F)
Method	1	2.53	2.53	8.39	0.12	0.001
Year	2	1.61	0.81	2.67	0.077	0.001
Region	2	1.39	0.70	2.30	0.07	0.001
Residuals	51	15.45	0.30		0.74	

Table 3. Results of PERMANOVA using Morisita–Horn distances across Pennsylvania apple orchards (2012–2014)

	d.f.	Sums of sqs	Mean sqs	F.Model	R ²	Pr(>F)
Method	1	2.02	2.02	7.85	0.23	0.001
Year	2	0.75	0.37	1.45	0.08	0.091
Residuals	24	6.17	0.26	0.69		

(Buchanan et al. 2017), despite the fact that this species is a strict oligolege of Cucurbitaceae and that potato does not provide nectar resources. However, BVTs did remarkably well in matching bumble bee observations in red clover fields (Rao and Stephen 2009), and the performance in Pennsylvania apple orchards reported here had more overlapping species with nets than did the Michigan sour cherry study. Thus, it seems that crop- and region-specific results can be expected if using BVTs to monitor bee communities, and they should not automatically be considered for a low-input approach to monitoring bees in crop fields or other habitats.

A recent study suggests that passive sampling for bees using colored bowls does not impact bee communities, owing to consistent communities being found over multiple years and at similar sites never before sampled (Gezon et al. 2015). Our results suggest that this may not be true of BVTs, as the extremely high abundance of some bee species captured may be problematic. In the most extreme case from our study, over 1,000 *L. pilosum* were captured in Michigan using 40 BVTs in 2014, followed by a combined 52 specimens trapped in the next 2 yr. *Lasioglossum* have extended

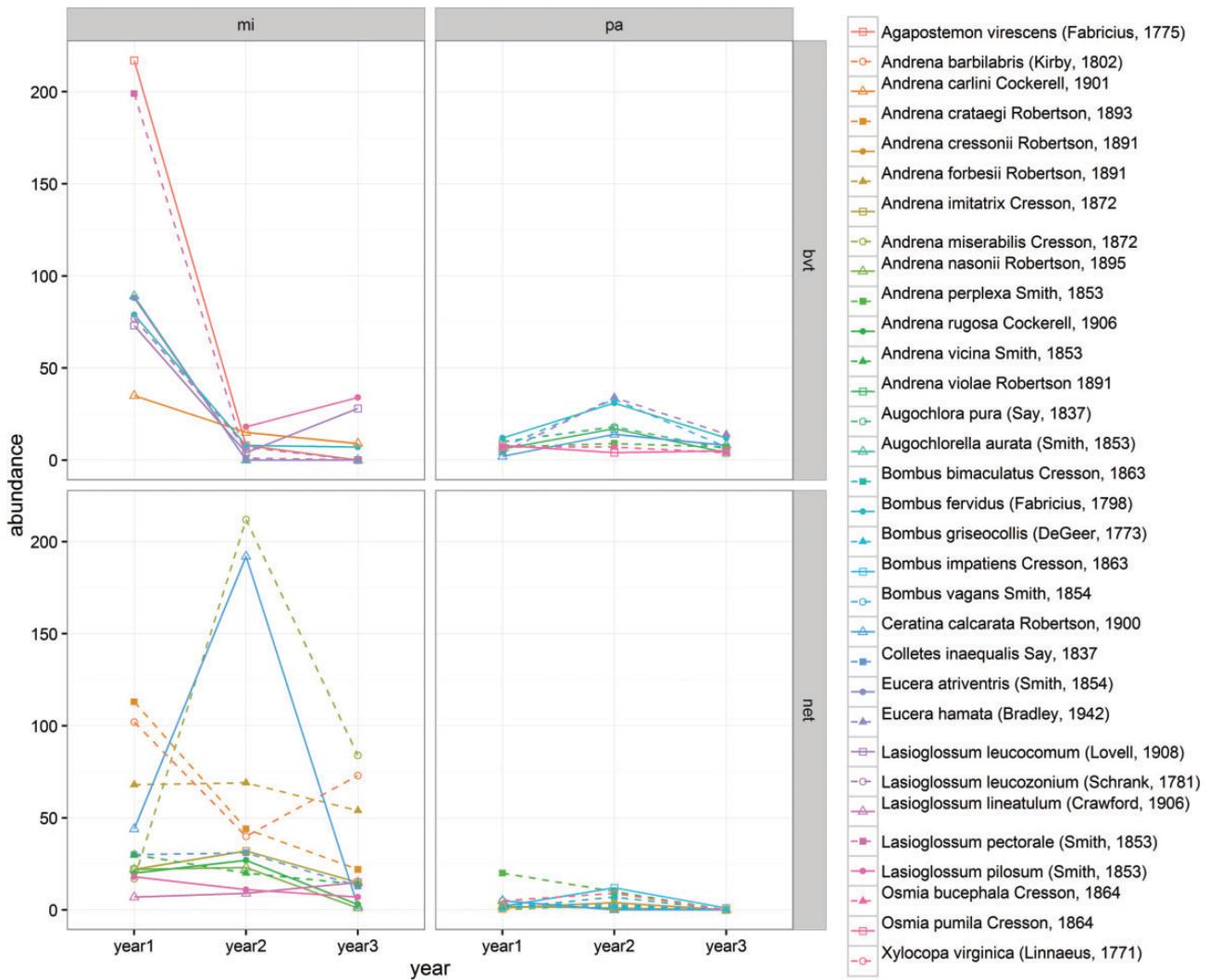


Fig. 5. Abundance of bee species collected in Michigan cherry (mi) and Pennsylvania apple (pa) that cumulatively accounted for 80% of total captures from blue vane traps (bvt) and net collections (net) over 3 yr of sampling (2014–2016 in Michigan and 2012–2014 in Pennsylvania). *Lasioglossum pilosum* is excluded from Michigan bvt data for purposes of scale.

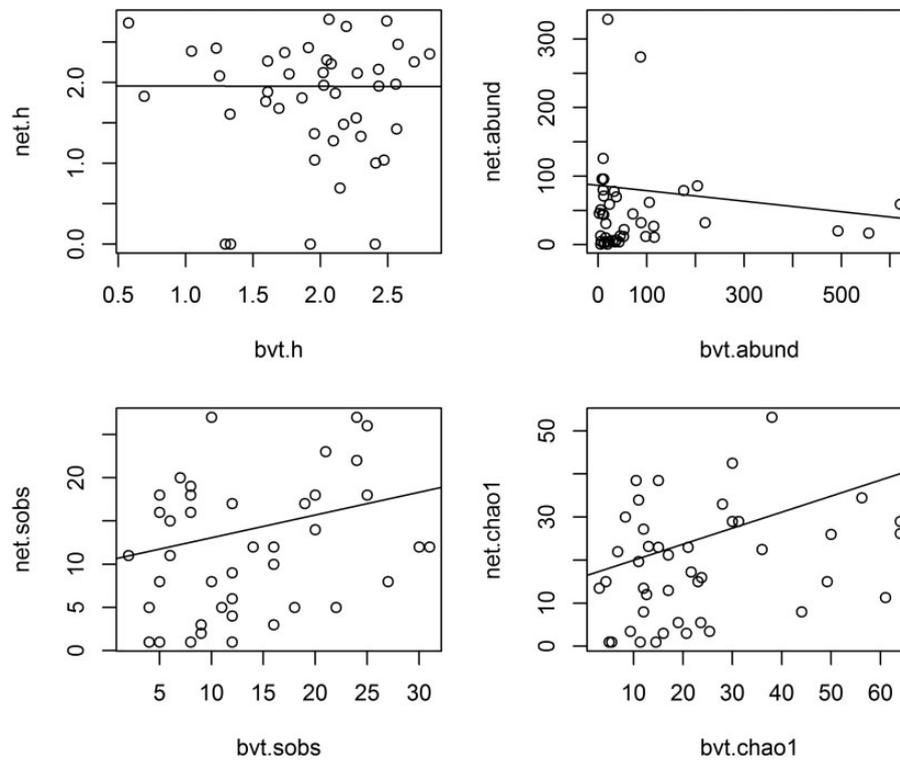


Fig. 6. Relationship between blue vane trap (bvt) captures and net collections for bee diversity (h), abundance (abund), observed species richness (sobs), and Chao-1 predicted richness (chao1) across tree fruit orchards in Pennsylvania and Michigan.

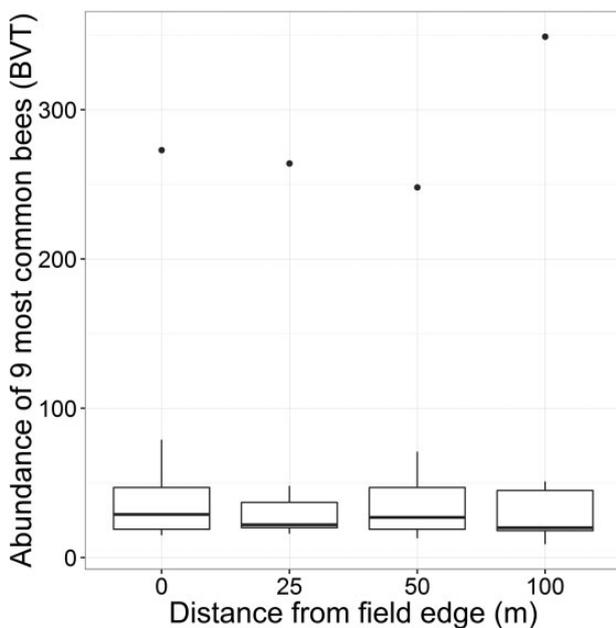


Fig. 7. Abundance by distance of the nine most abundant bee species captured in blue vane traps (BVT) from Michigan sour cherry orchards, cumulatively accounting for 80% of all individuals in traps. No significant effect of distance was found.

phenologies, with male production and mating limited to the late summer (Michener 1974), so the bees we captured in early spring would not be capable of any level of reproductive output during that season. *Bombus* are readily captured by BVTs, which is potentially advantageous for biodiversity surveys, as they are relatively infrequent in bowl captures (Droege et al. 2010). However, in the early spring, all

individual *Bombus* are gynes without the behavioral capacity for effective reproduction at this early stage of the season (Michener 1974, Williams et al. 2014). *Eucera hamata* and *E. atriventris* are solitary species, but are relatively uncommon in our region excluding BVTs. *Eucera hamata* was not included in a recent checklist for Pennsylvania bees (Donovall and VanEngelsdorp 2010), but this species has been collected in great abundance in recent pollinator surveys using BVTs. Michigan and Pennsylvania are near the northern limits of the range of *E. hamata*, although its range may be extending northward (Zarrillo et al. 2016). Both species were collected in high relative abundance in 2014, but none were captured in subsequent years. The majority of individuals collected were males, so if these collections are impacting local populations it is presumably through access to mates. Such dramatic declines were not observed in the genus *Andrena*, which is typically the most abundant group in net collections in Midwestern and northeastern orchards (Watson et al. 2011, Martins et al. 2015, Russo et al. 2015). *Andrena* were infrequently collected in BVTs relative to nets in our sour cherry orchards, although similar numbers were captured with both methods in Pennsylvania apple. A large number of *Eucera* (507) were also captured in 2015 in Pennsylvania cherry orchards, and preliminary examination of collections from 2016 suggest that capture rates were reduced by >40%.

An alternative explanation for the declining captures of particular species over time in the BVTs from Michigan is that the traps were becoming less attractive to bees as they aged. Plastic can be degraded by exposure to ultraviolet light, and the UV reflecting pigments used in these traps (Stephen and Rao 2005) may degrade over time. However, studies by Joshi et al. (2015) have demonstrated that traps retain their reflectance characteristics after several months of deployment in orchards. Additionally, the dramatic declines evident in Michigan cherry orchards were not seen in Pennsylvania apple orchards using the same trap design. The fewer sites sampled in Pennsylvania and the lower

number of captures overall may have limited our power to find differences in this region. In fact, the only significant effects in Pennsylvania by year were seen as an increase in abundance between 2012 and 2013. It should be noted that 2012 was an extremely early spring in Pennsylvania, with spring-flying bees emerging in March, a full month early. This was followed by seasonal cold temperatures in April that damaged flowers and prevented bee flight. The low captures in 2012 may be owing in part to this phenomenon.

In a 2-yr prairie study using BVTs, Kimoto et al. (2012) also captured many fewer *Bombus* and *Lasioglossum* in the second year. Substantially fewer bees were captured in subsequent years of a study in Pennsylvania by Joshi et al. (2015) that included BVTs, but this also coincided with severe weather conditions in the second year that potentially impacted the bee community over the same time period. Bee populations fluctuate from year-to-year and make detecting long-term change quite challenging (Williams et al. 2001). Therefore, to rule out natural annual variation, additional multiyear studies using BVTs in different habitat types and at different times of the season should be conducted to determine whether there are settings in which the negative effects on wild bees reported here are not apparent. However, our results clearly demonstrate that BVTs are not an effective method for sampling bee communities associated with crop plants. It is recommended that BVTs not be used as proxies for measuring communities responsible for pollination services. Furthermore, there is strong evidence that BVTs may negatively affect those bee species that they preferentially capture. The effectiveness of BVTs means they have value for sampling bee communities in other contexts. However, they should be used with care (e.g., limiting the number and duration of use) or excluded from sampling protocols in favor of other less destructive methods, like bee bowls (Gezon et al. 2015), in areas where bee populations may be sensitive to local extirpation or when at-risk species, such as *Bombus affinis* Cresson (Hatfield et al. 2016), are known to be present.

Acknowledgments

This research was supported by the United States Department of Agriculture-National Institute of Food and Agriculture, Specialty Crop Research Initiative, Project 2012-51181-20105: Developing Sustainable Pollination Strategies for US Specialty Crops. Additional support for Pennsylvania apple research came from USDA-NIFA-SCRI Grant PEN04398: Determining the Role of and Limiting Factors Facing Native Pollinators in Assuring Quality Apple Production in Pennsylvania; a Model for the Mid-Atlantic Tree Fruit Industry and the State Horticultural Association of Pennsylvania. We thank two anonymous reviewers for their helpful suggestions to improve the manuscript.

References Cited

- Allsopp, M. H., J. de Lange, and R. Veldtman. 2008. Valuing insect pollination services with cost of replacement. *PLoS ONE* 3: e3128.
- Andrus, R., and S. Droege. 2016a. Draft guide to the *Eucera* of Eastern North America. Discover Life. (<http://www.discoverlife.org/mp/20q?guide=Eucera>) (accessed 20 March 2017).
- Andrus, R., and S. Droege. 2016b. Draft guide to the *Stelis* of Eastern North America. Discover Life. (<http://www.discoverlife.org/mp/20q?guide=Stelis>) (accessed 20 March 2017).
- Atwood, C. E. 1933. Studies on the Apoidea of western Nova Scotia with special reference to visitors of apple bloom. *Can. J. Res.* 9: 443–457.
- Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, and R. Winfree. 2013. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecol. Lett.* 16: 1331–1338.
- Blitzer, E. J., J. Gibbs, M. G. Park, and B. N. Danforth. 2016. Pollination services for apple are dependent on diverse wild bee communities. *Agric. Ecosyst. Environ.* 221: 1–7.
- Bouseman, J. K., and W. E. LaBerge. 1979. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IX. Subgenus *Melandrena*. *Trans. Am. Entomol. Soc.* 104: 275–389.
- Boyle, R.M.D., and B.J.R. Philogene. 1983. The native pollinators of an apple orchard: Variations and significance. *J. Hortic. Sci.* 58: 355–363.
- Buchanan, A. L., J., Gibbs, L., Komondy, and Z., Szendrei 2017. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. *Insects* 8: 30.
- Christopoulos, D. T. 2012. Developing methods for identifying the inflection point of a convex/concave curve. <https://arxiv.org/abs/1206.5478> (accessed 20 March 2017)
- Christopoulos, D. T. 2016. Inflection: Finds the inflection point of a curve. R package version 1.2.
- Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. *Proc. R. Soc. Lond. B Biol. Sci.* 205.
- Delaplane, K. S., and D. F. Mayer. 2000. Crop pollination by bees. CABI Publishing, New York, NY.
- Donovall, L. R., and D. VanEngelsdorp. 2010. A checklist of the bees (Hymenoptera: Apoidea) of Pennsylvania. *J. Kans. Entomol. Soc.* 83: 7–24.
- Droege, S. 2016. *Nomada*. Discover Life. (<http://www.discoverlife.org/mp/20q?search=Apoidea>) (accessed 20 March 2017).
- Droege, S., and S. Rehan. 2016. Guide to the *Ceratina* of Eastern North America. Discover Life. (<http://www.discoverlife.org/mp/20q?guide=Ceratina>) (accessed 20 March 2017).
- Droege, S., V. J. Tepedino, G. LeBuhn, W. Link, R. L. Minkley, Q. Chen, and C. Conrad. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conserv. Divers.* 3: 15–23.
- Droege, S., and E. Tucker. 2016. Draft guide to the *Bombus* of Eastern North America. Discover Life. (<http://www.discoverlife.org/mp/20q?search=Apoidea>) (accessed 20 March 2017).
- Free, J. B. 1993. Insect pollination of crops. Harcourt Brace Jovanovich, London, United Kingdom.
- Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339: 1608–1611.
- Garratt, M.P.D., D. Breeze, N. Jenner, C. Polce, J. C. Biesmeijer, and S. G. Potts. 2014. Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agric. Ecosyst. Environ.* 184: 34–40.
- Garratt, M.P.D., D. Breeze, V. Boreux, M. T. Fountain, M. Mc Kerchar, S. M. Webber, D. J. Coston, N. Jenner, R. Dean, D. B. Westbury, et al. 2016. Apple pollination: Demand depends on variety and supply depends on pollinator identity. *PLoS ONE* 11: e0153889.
- Geroff, R. K., J. Gibbs, and K. W. McCravy. 2014. Assessing bee (Hymenoptera: Apoidea) diversity of an Illinois restored tallgrass prairie: Methodology and conservation considerations. *J. Insect Conserv.* 18: 951–964.
- Gezon, Z. J., S. Wyman, J. S. Ascher, D. W. Inouye, and R. E. Irwin. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods Ecol. Evol.* 6: 1044–1054.
- Gibbs, J. 2011. Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa* 1–216.
- Gibbs, J., L. Packer, S. Dumes, and B. N. Danforth. 2013. Revision and reclassification of *Lasioglossum* (*Eurylaeus*), *L.* (*Hemihalictus*) and *L.* (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa* 3672: 1–117.
- Gibbs, J., E. Elle, K. Bobiwash, T. Haapalainen, and R. Isaacs. 2016. Contrasting pollinators and pollination in native and non-native regions of highbush blueberry production. *PLoS ONE* 11: e0158937.
- Griswold, T. L., H. Ikerd, S. Droege, and J. B. Pascarella. 2016. Draft guide to the *Osmia* of Eastern North America. Discover Life. (<http://www.discoverlife.org/mp/20q?search=Apoidea>) (accessed 20 March 2017).
- Gwynne, D. T., and D.C.F. Rentz. 1983. Beetles on the bottle: Male buprestids mistake stubbies for females (Coleoptera). *Aust. J. Entomol.* 22: 79–80.
- Hansted, L., B.W.W. Grout, T. B. Toldam-Andersen, and J. Eilenberg. 2015. Effectiveness of managed populations of wild and honey bees as supplemental pollinators of sour cherry (*Prunus cerasus* L.) under different climatic conditions. *Acta Agric. Scand. Sect. B—Soil Plant Sci.* 65: 109–117.

- Hatfield, R., S. Jepsen, R. Thorp, L. Richardson, and S. Colla. 2016. *Bombus bohemicus*. IUCN Red List Threat. Species.
- Heinrich, B. 1976. Resource partitioning among some eusocial insects: Bumblebees. *Ecology* 57: 874–889.
- Isaacs, R., and A. K. Kirk. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J. Appl. Ecol.* 47: 841–849.
- Joshi, N. K., T. Leslie, E. G. Rajotte, M. A. Kammerer, M. Otieno, and D. J. Biddinger. 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Ann. Entomol. Soc. Am.* 108: 785–799.
- Joshi, N. K., M. Otieno, E. G. Rajotte, S. J. Fleischer, and D. J. Biddinger. 2016. Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. *Front. Ecol. Evol.* 4: 38.
- Kearns, C. A., and J. D. Thomson. 2001. The natural history of bumblebees: A sourcebook for investigations. University Press of Colorado, Boulder, CO.
- Kimoto, C., S. J. Debano, R. W. Thorp, S. Rao, and W. P. Stephen. 2012. Investigating temporal patterns of a native bee community in a remnant North American bunchgrass prairie using blue vane traps. *J. Insect Sci.* 12: 1–12.
- Kleijn, D., R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, A. M. Klein, C. Kremen, L. K. M'Gonigle, R. Rader, et al. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6: 7414.
- LaBerge, W. E. 1971. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IV. *Scapteropsis*, *Xiphandrena* and *Raphandrena*. *Trans. Am. Entomol. Soc.* 97: 441–520.
- LaBerge, W. E. 1973. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part VI. Subgenus *Trachandrena*. *Trans. Am. Entomol. Soc.* 99: 235–371.
- LaBerge, W. E. 1977. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part VIII. Subgenera *Thysandrena*, *Dasyandrena*, *Psammandrena*, *Rhacandrena*, *Euandrena*, *Oxyandrena*. *Trans. Am. Entomol. Soc.* 103: 1–143.
- LaBerge, W. E. 1980. A revision of the bees of the genus *Andrena* of the western hemisphere. Part X. Subgenus *Andrena*. *Trans. Am. Entomol. Soc.* 106: 395–525.
- LaBerge, W. E. 1987. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliandrena*, and *Melandrena*. *Trans. Am. Entomol. Soc.* 112: 191–248.
- LaBerge, W. E. 1989. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XIII. Subgenera *Simandrena* and *Taeniandrena*. *Trans. Am. Entomol. Soc.* 115: 1–56.
- LaBerge, W. E., and J. K. Bouseman. 1970. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part III. *Tylandrena*. *Trans. Am. Entomol. Soc.* 96: 543–605.
- LaBerge, W. E., and D. W. Ribble. 1975. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part VII. Subgenus *Euandrena*. *Trans. Am. Entomol. Soc.* 101: 371–446.
- Larkin, L. L., R. Andrus, and S. Droege. 2016. *Andrena*. Discover Life. (<http://www.discoverlife.org/mp/20q?search=Apoidea>) (accessed 20 March 2017).
- Laverty, T. M., and L. D. Harder. 1988. The bumble bees of eastern Canada. *Can. Entomol.* 120: 965–967.
- Mallinger, R. E., and C. Gratton. 2015. Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *J. Appl. Ecol.* 52: 323–330.
- Martins, K. T., A. Gonzalez, and M. J. Lechowicz. 2015. Pollination services are mediated by bee functional diversity and landscape context. *Agric. Ecosyst. Environ.* 200: 12–20.
- McGinley, R. J. 2003. Studies of Halictinae (Apoidea: Halictidae), II: Revision of *Sphecodogastra* Ashmead, floral specialists of Onagraceae. *Smithson. Contrib. to Zool.* 610: 1–55.
- McGregor, S. E. 1976. Insect pollination of cultivated crop plants, Agriculture Handbook No. 496. Agricultural Research Service, USDA, Washington, DC.
- Medler, J. T. 1962. Morphometric studies on bumble bees. *Ann. Entomol. Soc. Am.* 55: 212–218.
- Michener, C. D. 1974. The social behavior of the bees. Belknap Press, Cambridge, MA.
- Michener, C. D. 2000. The bees of the world. The Johns Hopkins University Press, Baltimore.
- Michener, C. D., J. McGinley, and B. N. Danforth. 1994. The Bee Genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC.
- Mitchell, T. B. 1960. Bees of the Eastern United States: Volume I. N. C. Agric. Exp. Stn. Tech. Bull. 141: 1–538.
- Mitchell, T. B. 1962. Bees of the Eastern United States: Volume II. N. C. Agric. Exp. Stn. Tech. Bull. 152: 1–557.
- Mogren, C. L., A. Rand, S. W. Fausti, and J. G. Lundgren. 2016. The affects of crop intensification on the diversity of native pollinator communities. *Environ. Entomol.* 45: 865–872.
- Oksanen, J., G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, F. L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2013. Vegan: Community Ecology Package. R package version 2.0-10.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120: 321–326.
- Park, M. G., A. Raguso, J. E. Losey, and B. N. Danforth. 2016. Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards. *Apidologie* 47: 145–160.
- R Core Team. 2015. R: A language and environment for statistical computing. R version 3.2.2. R Found. Stat. Comput.
- Rao, S., and W. P. Stephen. 2009. Bumble bee pollinators in red clover seed production. *Crop Sci.* 49: 2207–2214.
- Rao, S., W. P. Stephen, and L. White. 2009. Native bee pollinator diversity in Oregon blueberries, pp. 539–48. In K. E. Hummer, B. C. Strik, and C.E. Finn (eds.), Proc. IXth Int. Vaccinium Symp. International Society for Horticultural Science, Corvallis, OR.
- Rehan, S. M., and C. S. Sheffield. 2011. Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. *Zootaxa* 2873: 35–50.
- Russo, L., N. Debarros, S. Yang, K. Shea, and D. Mortensen. 2013. Supporting crop pollinators with floral resources: Network-based phenological matching. 1–16.
- Russo, L., M. Park, J. Gibbs, and B. Danforth. 2015. The challenge of accurately documenting bee species richness in agroecosystems: Bee diversity in eastern apple orchards. *Ecol. Evol.* 5: 3531–3540.
- Stephen, W. P., and S. Rao. 2005. Unscented color traps for non-*Apis* bees (Hymenoptera: Apiformes). *J. Kansas Entomol. Soc.* 78: 373–380.
- Stephen, W. P., and S. Rao. 2007. Sampling native bees in proximity to a highly competitive food resource (Hymenoptera: Apiformes). *J. Kansas Entomol. Soc.* 80: 369–376.
- Stephen, W. P., S. Rao, and L. White. 2009. Abundance, diversity and foraging contribution of bumble bees to blueberry production in western Oregon. *Acta Hort.* 810: 557–562.
- Timberlake, P. H. 1969. A contribution to the systematics of North American species of *Synhalonia* (Hymenoptera, Apoidea). *Univ. Calif. Publ. Entomol.* 57: 1–76.
- Watson, J. C., T. Wolf, and J. S. Ascher. 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environ. Entomol.* 40: 621–632.
- Williams, N. M., L. Minckley, and F. A. Silveira. 2001. Variation in native bee faunas and its implications for detecting community changes. *Conserv. Ecol.* 5: 7.
- Williams, P. H., W. Thorp, L. L. Richardson, and S. R. Colla. 2014. Bumble bees of North America: An identification guide. Princeton University Press, Princeton, NJ.
- Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* 18: 626–635.
- Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. B.* 276: 229–237.
- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* 45: 793–802.
- Zarrillo, T. A., S. Ascher, J. Gibbs, and K. A. Stoner. 2016. New and noteworthy records of bees (Hymenoptera: Apoidea: Anthophila) for Connecticut. *J. Kans. Entomol. Soc.* 89: 138–157.