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ORIGINAL PAPER

Pesticide use within a pollinator-dependent crop has negative effects on the abundance and species richness of sweat bees, *Lasioglossum* spp., and on bumble bee colony growth

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Abstract Pesticides are implicated in current bee declines. Wild bees that nest or forage within agroecosystems may be exposed to numerous pesticides applied throughout their life cycles, with potential additive or synergistic effects. In pollinator-dependent crops, pesticides may reduce bee populations, creating trade-offs between pest management and crop pollination. In this three-year study, we examined the effects of pesticides on the abundance and species richness of wild bees within apple orchards of southern Wisconsin. We additionally deployed colonies of *Bombus impatiens*, a native and common species, in order to relate colony performance to orchard pesticide use. Utilizing grower spray records, we developed "toxicity scores" as a continuous index of pesticide use for each orchard, a measure that incorporated each pesticide's relative toxicity to bees, its residual activity, and its application rate. While there was no relationship between total wild bee abundance and species richness with toxicity scores, there was a significant, negative effect on sweat bees, *Lasioglossum* spp. Many of these sweat bees are small-bodied, have short foraging ranges, are social, and have long foraging periods, all traits that could increase bee exposure or sensitivity to orchard pesticides. In addition, sentinel bumble bee colonies at orchards with high toxicity scores produced fewer, and smaller, workers. Bumble bees may also have a greater sensitivity and exposure to orchard pesticides due to their sociality and long foraging periods. Our results demonstrate that certain bee taxa may have a higher exposure or sensitivity to on-farm pesticide applications, and could therefore be vulnerable in agroecosystems.

Keywords Toxicity · Native bee · *Bombus* · Apple · Orchard · Pest management · Organic

Introduction

Agricultural intensification, and associated increases in pesticide use, may be causing declines in wild bee populations (Biesmeijer et al. 2006; National Research Council 2007; Colla and Packer 2008; Potts et al. 2010; Burkle et al. 2013). These wild bees are essential for the pollination of many crops, and thus their status within agricultural landscapes is important for the global food supply (Gallai et al. 2009; Eilers et al. 2011; Garibaldi et al. 2013). In agricultural landscapes, bees may encounter a combination of pesticides that influence their behavior and fitness. The overall effect of these pesticides is in part determined by the toxicity of a pesticide's active ingredient and the bees' level of exposure. Pesticide exposure varies due to many factors including bees' foraging behaviors and the timing of pesticide applications. It is therefore important to examine the impact of pest management within working farms and under natural bee foraging conditions. The objectives of this study were to explore the relationship between pesticide use within apple orchards and the abundance and species richness of wild bees during crop bloom, and to determine the effects of pesticide

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applications on the growth and reproductive output of bumble bee colonies residing within orchards.

Pesticides can impact wild bees through both direct lethal effects, and through sublethal effects on bee behavior and physiology (Desneux et al. 2007). Studies examining direct effects have found that many pesticides applied at recommended doses do not kill honey bees or other managed bees (Morandin and Winston 2003; Ladurner et al. 2005; Morandin et al. 2005; Abbott et al. 2008; Cresswell 2011; Baron et al. 2014). The indirect effects of pesticides on bees are generally less well known but may be as influential as direct, lethal effects. For example, pesticide exposure to social bees, including bumble bees and honey bees, can affect foraging performance (Morandin et al. 2005; Gill et al. 2012; Whitehorn et al. 2012; Larson et al. 2013). In particular, neonicotinoid insecticides impair the homing and learning abilities of worker bees, and reduce overall foraging efficacy (Morandin and Winston 2003; Yang et al. 2008; Mommaerts et al. 2010; Cresswell 2011; Henry et al. 2012; Williamson and Wright 2013; Rundlöf et al. 2015; but see Tasei et al. 2001). Insecticide exposure may also delay bee development, having potential consequences for population growth rates (Abbott et al. 2008; Wu et al. 2011). Furthermore, negative, synergistic effects on bees occur when there is exposure to multiple pesticides, or when pesticide exposure is combined with other stressors such as pathogens (Wahl and Ulm 1983; Pilling and Jepson 1993; Fauser-Misslin et al. 2014; Pettis et al. 2013; Williamson and Wright 2013; Zhu et al. 2014). Therefore, in addition to measuring the isolated impacts of individual pesticides, studies are needed that consider the combined direct, indirect, short-term and long-term effects of pest management on bees. One approach to examining the overall effects of pesticides on bees is to compare on-farm wild bee populations across gradients in pesticide use.

The effects of pesticides on bees can vary among taxa, depending on life-history traits such as level of sociality, body size, and foraging period or specialization (Brittain and Potts 2011; Arena and Sgolastra 2014). For example, pesticide use was found to have greater negative effects on social bees compared to solitary bees (Williams et al. 2010). This may be due to social species' longer foraging periods, which result in exposure to numerous, diverse pesticides throughout the growing season. Small-bodied bees may also be more affected by certain pesticides as lethal doses for small-bodied organisms are lower than those for large-bodied ones (Thompson and Hunt 1999; Malone et al. 2000). Furthermore, differences among bee species in their diet breadths, foraging preferences, and foraging ranges will affect their exposure to pesticides. Bee species with short foraging ranges may be more affected by pesticides applied at local spatial scales (single farms), while species with longer foraging ranges may be more sensitive to applications at the landscape scale (across multiple ecosystems) (Brittain and Potts 2011). Additionally, specialist bees may be more vulnerable to pesticides applied on their preferred food source relative to generalists that forage on a diversity of plants (Brittain and Potts 2011). Thus, predicting the overall effects of pesticides on wild bee communities and pollination services requires an understanding of which bee taxa are at greater risk.

Many previous studies examining the effects of pesticides on bees have compared organic and conventional cropping systems. Organic farms, or regions with a high proportion of organic farms, are often associated with a higher abundance and diversity of bees and higher pollination rates (Kremen et al. 2002; Morandin and Winston 2005; Holzschuh et al. 2007, 2008; Andersson et al. 2012; Kennedy et al. 2013; but see Kremen et al. 2004; Shuler et al. 2005; Brittain et al. 2010). However, organic and conventional farms differ not only in pesticide use, but in other attributes including farm size, crop diversity, and location. In particular, organic farms tend to have higher on-farm plant diversity, and/or are located within more complex landscapes (Holzschuh et al. 2008, 2010). Therefore, in comparing organic to conventional farms, it is difficult to differentiate the relative influence of pesticides on bees from other farm characteristics. Previous studies examining the effect of pesticides on bees across a continuous gradient, using a calculated toxicity score, found negative effects of pesticide toxicity on wild bee abundance and diversity, though responses varied by year and bee taxa (Tuell and Isaacs 2010; Park et al. 2015). A continuous index of pesticide toxicity takes into consideration the variability within and across farming systems (organic and conventional), and may thus better represent potential pesticide risks to bees.

In this research, we examined the effects of pest management practices on local wild bee communities within apple orchards of southern Wisconsin, USA, using a continuous metric of pesticide toxicity ("toxicity scores"). Farms in this area practiced a range of management strategies that created a large gradient in these toxicity scores. We analyzed responses by the entire wild bee community as well as taxon-specific responses by common bee genera. Additionally, we explored the relationship between toxicity scores and colony performance of sentinel bumble bees as a way to more directly assess the cumulative effects of pesticides on individual bee and colony level responses. We hypothesized that orchards with higher toxicity scores would have lower total wild bee abundance and species richness due to the combined short-term (within-year) and long-term (previous years) effects of pesticide use on bee populations. We additionally hypothesized that sentinel bumble bee colony weight gain, queen production, and worker production would be negatively related to toxicity scores.

Methods

Study sites and experimental design

Apple orchards selected for this study ranged in pest management approaches. These included a total of four no-input orchards (no pesticides), six organic orchards (using only USDA certified organic pesticides), and 15 conventional orchards (using non-organic pesticides, but varying in the number of pesticide applications per year). All orchard study sites were located in southern Wisconsin at least 5 km from any other site, a distance greater than most bees' foraging ranges (Gathmann and Tscharntke 2002; Greenleaf et al. 2007), in order to ensure independence of measurements (Supplementary material 1). We additionally selected orchards so that pest management philosophy, i.e. organic/no-input versus conventional, was not related to the percentage of cropland (all agricultural land-cover categories excluding pasture) in the surrounding 1 km landscape as measured using remotely-sensed land-cover data (2010 National Agricultural Statistics Service Cropland Data Layer) in ArcMap 9.2 (Esri 2009) ($t_{27} = -0.81$, $P = 0.21$). This was done in order to ensure that any effects of orchard pest management on bees would be independent of the possible effects from agricultural management in the surrounding landscape. Over three growing seasons (2010, 2012 and 2013), we developed toxicity scores from spray records, and measured wild bee abundance and species richness. Over two growing seasons (2012 and 2013), we assessed individual and colony-level traits of sentinel bumble bees placed within the orchards.

Calculation of toxicity scores

At the end of each growing season, we obtained grower-supplied spray records for each of the orchards sampled in that year for a total of 48 unique records (16 in 2010, 15 in 2012, and 17 in 2013). All records contained the application rate and date of pesticides applied throughout the entire growing season (March–October), including all herbicides, fungicides, and insecticides. We calculated a comprehensive, full-season toxicity score for each orchard using the Environmental Impact Quotient (EIQ) Field Use Rating formula (Eq. 1), which takes into account the pesticide's relative toxicity to bees and the amount of active ingredient applied within the orchard (Kovach et al. 1992). To determine the quantity of each active ingredient applied, we multiplied the application rate (oz of weight/acre) by the percent of the principal active ingredient for each pesticide. We then multiplied this quantity by the "bee-toxicity value" for the active ingredient listed in the 2010 EIQ database (Eshenaur et al. 2010) (Supplementary material 2). The bee-toxicity value for individual pesticide active ingredients is the product of the active ingredient's acute toxicity to honey bees on a scale of 1–5 (relatively nontoxic = 1 ($LD_{50} > 100$ µg/bee), moderately toxic = 3 ($LD_{50} = 2$–10.99 µg/bee), highly toxic = 5 ($LD_{50} < 2$ µg/bee)) and its plant surface residue half-life on a scale of 1–5 (1–2 weeks = 1, 2–4 weeks = 3, >4 weeks = 5) (Kovach et al. 1992). Compounds assumed to be nontoxic to bees and/or with unknown toxicity, including adjuvants and fertilizers, were not included in the scores. This process was repeated for each application at each orchard during a season, to obtain the cumulative, full-season toxicity score for the orchard (Eq. 1):

$$\begin{aligned}\text{Toxicity Score} = \sum [&\text{Rate (oz of weight/acre)} \\ &\times \text{Percent active ingredient} \\ &\times \text{EIQ bee toxicity value}]\end{aligned} \tag{1}$$

We additionally calculated early-season toxicity scores for each orchard in each year using the above Eq. 1, but including only pesticides that were applied from the beginning of the year through the end of our sampling period, which occurred during apple bloom of each year. These early-season toxicity scores may indicate the within-year, or immediate, effects of pesticides on wild bees sampled during the apple bloom period. Full-season toxicity scores, on the other hand, may indicate overall differences in pest management, which, if consistent over time, could be expected to have persistent, long-term effects on wild bees, especially on species that forage past the apple bloom period.

Wild bee sampling

Wild bees were collected with bee traps at the same orchards from which we obtained spray records in 2010, 2012 and 2013. We sampled bees during the apple-bloom period, which occurs for 1–3 weeks between mid April and late May, since wild bees are active within orchards during this period and are important for apple production (Mallinger and Gratton 2015). Bee traps were made with 355 ml white plastic cups (Solo Cup Co., Urbana, IL) painted fluorescent blue, fluorescent yellow, or left white, and filled with a 20 % propylene glycol and 1 % unscented dish soap solution. At each site, we hung ten bee traps of alternating white, yellow and blue color from stakes at mid-canopy height, approximately 1.5 m above ground. We placed the stakes within two interior tree rows, 20 m from any orchard edge, and separated from each other by 5 m. After 1 week in the field, we emptied the contents of bee traps and added new solution for each consecutive week of sampling during the bloom period (3 weeks in 2010, 2 weeks in 2012, and 1 week in 2013). All collected bees were stored in alcohol until they were pinned, dried, and identified to species with the assistance of expert taxonomists. We calculated total bee abundance and species richness for each orchard sampled in each year. We additionally calculated the abundance and species richness of the two dominant bee genera in apple orchards during apple bloom, *Andrena* spp. (mining bees), and *Lasioglossum* spp. (sweat bees), in order to look at taxon-specific responses to orchard pesticide use. No other bee genus was abundant or common enough to analyze separately (Supplementary material 3).

We used a model selection approach to analyze the effects of early-season and full-season toxicity scores on the abundance and species richness of all bees combined, *Andrena* spp., and *Lasioglossum* spp. (Burnham and Anderson 2004). Full-season toxicity scores were averaged across years for each orchard to represent average pesticide-use intensity, which was expected to have long-term or legacy effects on wild bees. Early-season toxicity scores were kept separate for each year in order to analyze possible immediate, within-year effects of pesticides on wild bees active during the apple bloom period. We ran separate model selection procedures for early-season and average full-season toxicity scores due to the strong correlation between these two predictor variables ($r = 0.81$). Predictor variables in the full model included fixed effects of year (2010, 2012, 2013), percent agriculture at a 1 km radius surrounding the orchard, and toxicity scores, either early-season or average full-season. We compared full models to models containing each of the predictor variables alone, and to models with all combinations of the predictor variables. Models with intercept only were used as null models. We calculated corrected Akaike Information Criterion, $\mathrm{AIC_c}$, values for all models for each response variable (abundance and richness of all bees combined, of *Andrena* spp., and of *Lasioglossum* spp., R version 3.1.2 MuMIn package). The model with the lowest $\mathrm{AIC_c}$ was considered to be the overall best-fit model ($\Delta\mathrm{AIC_c} = 0$), while models with $\Delta\mathrm{AIC_c} < 2$ were considered to be competing models (Burnham and Anderson 2004). We additionally calculated model weights, w, which represent the likelihood that each model would be the best-fit model in repeated runs of the experiment (R version 3.1.2 MuMIn package). Statistics for all models are presented in the results section, but for succinctness, parameter estimates and figures are from the overall best-fit models. Models for abundance of all bees, *Andrena* spp., and *Lasioglossum* spp. (all log-transformed), as well as total bee species richness (square-root transformed) were fit with linear models (R version 3.1.2 function "lm"), while *Andrena* and *Lasioglossum* species richness were fit with generalized linear models with Poisson distributions (R version 3.1.2 function "glm"). All models met assumptions of normality (linear models) and randomly distributed errors.

Bumble bee colony performance

The performance of sentinel bumble bee colonies placed within orchards was used as an indicator of an orchard's suitability for bees, complementing measurements of local wild bee abundance or diversity (Gibbs 2011). Unlike many wild bee species with short foraging periods, bumble bee colonies are active from the early spring through fall, and thereby potentially exposed to pesticides applied throughout the entire growing season. Furthermore, the placement of colonies within orchards ensures some exposure to on-farm pesticides. Additionally, the use of sentinel colonies allows the detection of individual and colony-level responses to pesticides.

We used commercial colonies of *Bombus impatiens*, a native and common species within our study area (Koppert Biological Systems, Howell, MI). Colonies were placed at 14 orchards in 2012 (seven conventional and seven organic/no-input) and at 14 orchards in 2013 (eight conventional and six organic/no-input), and were left for approximately 120 days in each year, from late March to July 2012 and from late April to August 2013, to coincide with the beginning of spring bloom and the period of pesticide applications. Bumble bee colonies started with one queen and approximately 30 workers at the beginning of the experiment. We weighed all colonies, including adults, immatures, brood, provisioning, occupied and empty brood cells, and the plastic nest box, to the nearest gram on the morning before they were deployed in the field. Each orchard received three colonies in 2012 and two colonies in 2013. After the majority of pesticides had been applied for the growing season, we brought colonies back to the lab and immediately placed them in a −80 °C freezer where they were stored until processed.

We re-weighed colonies, including all components weighed at the beginning of the experiment, and calculated weight gain as the difference between initial and final weight. We then measured gyne (new queen) production as either the number of gynes (in 2012), or the number of emerged gyne cells (in 2013). Colonies contained queen excluder doors in 2012, which allowed us to count gynes directly at the end of the season, but excluders were not used in 2013, which created more natural colony conditions by allowing gynes to permanently leave the colony after emergence. We also measured the production of workers and males in both years as the combined number of emerged worker and male cells. While we could distinguish gyne cells by their large size, we used a combined measure of workers and males because we were unable to differentiate between worker and male cells (Williams et al. 2012). Since males leave the colony shortly after emergence, and workers can die in the field during the season, the number of emerged cells may be a better estimate of worker and male production as compared to the number of bees within the colony at the time of collection. We then randomly selected approximately twenty worker bees from each colony and measured the distance between wing bases, or intertegular span, for each bee as an indicator of body size (Greenleaf et al. 2007). We averaged the colony and individual-level measurements per orchard.

To analyze the effects of toxicity scores on bumble bee colony performance, including weight gain, the average production of queens, the average combined production of workers and males, and average worker thorax width, we used the same model selection approach previously described. Predictor variables in the full model included year (2012, 2013), percent agriculture, and either early-season or full-season toxicity scores. We analyzed bumble bee responses to both toxicity scores as bumble bees may have greater exposure to sprays early in the season when there are few flowering resources available outside of the orchard, but are also likely to be exposed to season-long pesticide use due to their extended foraging periods. Linear models were created with log or square-root transformed response variables as necessary in order to meet assumptions of normality and randomly distributed errors (R version 3.1.2 function “lm”) and all model selection statistics were calculated with R version 3.1.2 package MuMIn.

Results

Pesticide toxicity scores

In each year, 45–65 different pesticides were applied across all orchards, with the number of applications ranging from 0 to 40 per orchard per year. No insecticides were applied during apple bloom, though fungicides were occasionally applied during bloom. Full-season toxicity scores did not significantly differ among the three study years ($F_{2,45} = 1.20$, $P = 0.31$). Moreover, full-season toxicity scores calculated from 2012 were positively correlated to full-season toxicity scores from 2013 at orchards sampled in both years ($n = 14$, $r = 0.88$, $P < 0.0001$), suggesting that an orchard’s relative season-long pesticide use may be consistent over time. Conventionally managed orchards had higher full-season toxicity scores (8953 ± 987) compared to organic orchards (3901 ± 1119) ($t_{46} = -3.38$, $P = 0.002$), though there was a large range in scores among both organic (0–23,209) and conventional (929–23,334) orchards.

Wild bee abundance and diversity

Across all study sites and years, 5673 wild bees were collected representing 80 different species (Supplementary material 3). Abundance of wild bees per orchard ranged from 20 to 1050 in 2010, 21–290 in 2012, and 7–61 in 2013, while species richness ranged from 9 to 28 in 2010, 6–23 in 2012, and 5–17 in 2013. We found no evidence of significant spatial autocorrelation for either wild bee abundance (Moran’s $I = -0.05$, $P = 0.22$) or wild bee species richness (Moran’s $I = 0.01$, $P = 0.20$). The most abundant genus was *Andrena* spp., representing 78 % of captured wild bees, followed by *Lasioglossum* spp., representing 9.5 % of the wild bee community. *Lasioglossum* was the most species rich genus, with 36 species, followed by *Andrena*, with 24 species. Other bee genera sampled during apple bloom included *Agapostemon*, *Augochlorella*, *Bombus*, *Ceratina*, *Colletes*, *Halictus*, *Megachile*, and *Osmia*.

Early-season toxicity scores and average full-season toxicity scores were not significant predictors of either total bee abundance or species richness; only year and percent agriculture were included in competing models (Table 1a, b). Year was the only predictor variable included in the overall best-fit model for total bee abundance, while for total bee species richness, the overall best-fit model included a negative effect of percent agriculture as well as an effect of year (Table 2a, b).

For taxon-specific responses, both early-season and average full-season toxicity scores, along with year and percent agriculture, were significant predictors of *Andrena* and *Lasioglossum* abundance and species richness (Table 1a, b). However, the two genera showed very different responses to toxicity scores. In the overall best-fit models, *Lasioglossum* abundance and species richness were negatively correlated to early-season and full-season toxicity scores (Fig. 1a–d), while *Andrena* species richness was positively correlated to early-season and full-season toxicity scores (Fig. 2a, b; Table 2a, b). Though the overall best-fit models for *Andrena* abundance did not contain either toxicity score, the toxicity scores were included in competing models (Tables 1a, b, 2a, b).

Bumble bee colony performance

On average, sentinel bumble bee colonies placed within orchards grew throughout their time in the field (4 months), though growth and reproductive output were highly variable. Nearly 90 % of colonies gained weight, with an average gain of 122 ± 22 g (mean ± SEM). The average number of new queens produced per colony was 12.8 ± 3.2, and the average combined number of workers and males produced per colony

Table 1 Model selection statistics for $i = 7$ models predicting the abundance and species richness of all wild bees (total abundance and richness), *Andrena* spp., and *Lasioglossum* spp. (Lasio.), trapped within apple orchards of southern Wisconsin during apple bloom, as a function of year, 2010, 2012 or 2013 (*Yr*), percent agriculture surrounding the orchard at a 1 km radius (*Ag*), and orchard toxicity scores (*Tox*) calculated as (a) early-season toxicity scores including sprays from the beginning of the year through apple bloom and (b) average full-season toxicity scores including all pesticide sprays applied during the growing season (March–October)

i	Explanatory variables	Log total abundance		Sqrt total richness		Log *Andrena* abundance		*Andrena* richness		Log Lasio. abundance		Lasio. richness	
		ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
(a) Early-season toxicity scores													
0	Intercept	31.9	0.00	24.0	0.00	37.2	0.00	39.3	0.00	8.6	0.01	13.8	0.00
1	*Yr*	**0.0**	**0.41**	**1.8**	**0.22**	3.1	0.12	4.9	0.06	3.5	0.11	8.0	0.01
2	*Tox*	34.1	0.00	26.3	0.00	38.1	0.00	35.2	0.00	7.4	0.02	7.0	0.02
3	*Ag*	33.8	0.00	24.9	0.00	38.3	0.00	38.6	0.00	10.9	0.00	14.0	0.00
4	*Tox* + *Yr*	2.3	0.13	3.8	0.08	5.3	0.04	4.8	0.06	**0.0**	**0.64**	**0.0**	**0.69**
5	*Tox* + *Ag*	36.0	0.00	27.1	0.00	38.4	0.00	31.8	0.00	9.7	0.00	8.9	0.01
6	*Ag* + *Yr*	**0.2**	**0.37**	**0.0**	**0.55**	**0.0**	**0.56**	2.3	0.21	5.9	0.03	7.8	0.01
7	*Tox* + *Ag* + *Yr*	2.9	0.10	2.6	0.15	**1.3**	**0.29**	**0.0**	**0.67**	2.6	0.18	**1.9**	**0.26**
(b) Average full-season toxicity scores													
0	Intercept	31.9	0.00	24.0	0.00	37.2	0.00	37.9	0.00	7.1	0.02	14.1	0.00
1	*Yr*	**0.0**	**0.41**	**1.8**	**0.22**	3.1	0.12	3.5	0.09	**1.9**	**0.20**	8.4	0.01
2	*Tox*	33.9	0.00	26.2	0.00	38.7	0.00	36.9	0.00	6.5	0.02	6.6	0.02
3	*Ag*	33.8	0.00	24.9	0.00	38.3	0.00	37.2	0.00	9.3	0.00	14.3	0.00
4	*Tox* + *Yr*	2.5	0.12	3.9	0.08	5.2	0.04	4.3	0.06	**0.0**	**0.54**	**0.0**	**0.67**
5	*Tox* + *Ag*	35.7	0.00	27.3	0.00	39.4	0.00	34.6	0.00	8.8	0.01	8.4	0.01
6	*Ag* + *Yr*	**0.2**	**0.36**	**0.0**	**0.55**	**0.0**	**0.54**	**0.9**	**0.33**	4.6	0.06	8.1	0.01
7	*Tox* + *Ag* + *Yr*	2.6	0.11	2.6	0.15	**1.2**	**0.30**	**0.0**	**0.52**	2.6	0.15	**1.8**	**0.28**

For each response variable, competing models ($\Delta AIC_c < 2$) are bolded

Table 2 Parameter estimates (β ± SE) from the best-fit models ($\Delta AIC_c = 0$) explaining the abundance and species richness of all wild bees (total abundance and richness), *Andrena* spp., and *Lasioglossum* spp. (Lasio.), trapped within apple orchards of southern Wisconsin during apple bloom

Explanatory variable	Log total abundance	Sqrt total richness	Log *Andrena* abundance	*Andrena* richness	Log Lasio. abundance	Lasio. richness
(a) Early-season toxicity scores						
Intercept	5.1 ± 0.2	4.4 ± 0.2	5.4 ± 0.3	2.4 ± 0.1	2.9 ± 0.3	1.8 ± 0.1
Tox				$2.6 \pm 1.2\ (\times 10^{-5})$	$-8.2 \pm 3.4\ (\times 10^{-5})$	$-6.4 \pm 2.1\ (\times 10^{-5})$
Yr						
(2012)	−0.8 ± 0.3	−0.6 ± 0.2	−1.6 ± 0.3	−0.3 ± 0.1	−0.6 ± 0.4	−0.3 ± 0.2
(2013)	−2.0 ± 0.3	−1.3 ± 0.2	−2.5 ± 0.3	−0.8 ± 0.1	−0.1 ± 0.3	−0.6 ± 0.2
Ag		−0.01 ± 0.0	−0.01 ± 0.0	$-5.8 \pm 2.2\ (\times 10^{-3})$		
(b) Average full-season toxicity scores						
Intercept	5.1 ± 0.2	4.4 ± 0.2	5.4 ± 0.3	2.4 ± 0.1	2.9 ± 0.3	1.9 ± 0.2
Tox				$1.9 \pm 1.0\ (\times 10^{-5})$	$-5.6 \pm 2.7\ (\times 10^{-5})$	$-4.8 \pm 1.5\ (\times 10^{-5})$
Yr						
(2012)	−0.8 ± 0.3	−0.6 ± 0.2	−1.6 ± 0.3	−0.4 ± 0.1	−0.4 ± 0.4	−0.2 ± 0.2
(2013)	−2.0 ± 0.3	−1.3 ± 0.2	−2.5 ± 0.3	−0.8 ± 0.1	−0.1 ± 0.3	−0.6 ± 0.2
Ag		−0.01 ± 0.0	−0.01 ± 0.0	$-5.7 \pm 2.2\ (\times 10^{-3})$		

Explanatory variables include year, 2010, 2012 and 2013, (*Yr*), percent agriculture at a 1 km radius surrounding the orchard (*Ag*), and orchard toxicity scores (*Tox*), calculated as (a) early-season toxicity scores including all pesticide sprays from the beginning of the year through apple bloom and (b) average full-season toxicity scores including all pesticide sprays applied during the growing season (March–October)

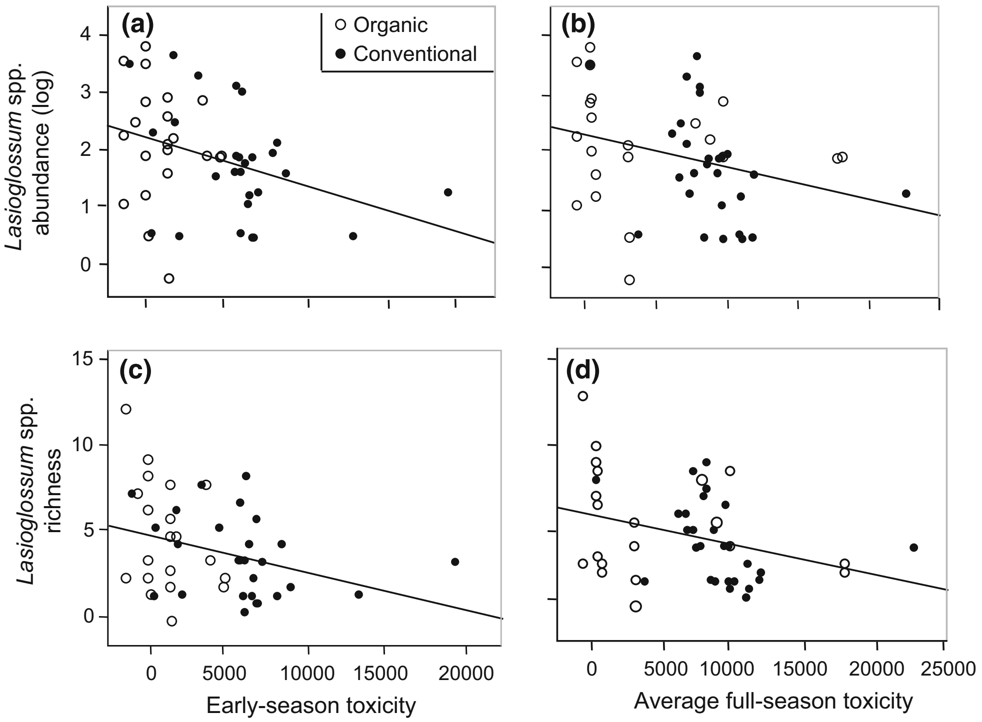

Fig. 1 Relationships between the abundance of *Lasioglossum* spp. and **a** early-season orchard toxicity scores and **b** average full-season orchard toxicity scores, and the species richness of *Lasioglossum* spp. with **c** early-season orchard toxicity scores and **d** average full-season orchard toxicity scores. Bees were trapped within apple orchards of southern Wisconsin during apple bloom in 2010, 2012 and 2013. Partial residual regression is from the best-fit model ($\Delta AIC_c = 0$) for each response variable

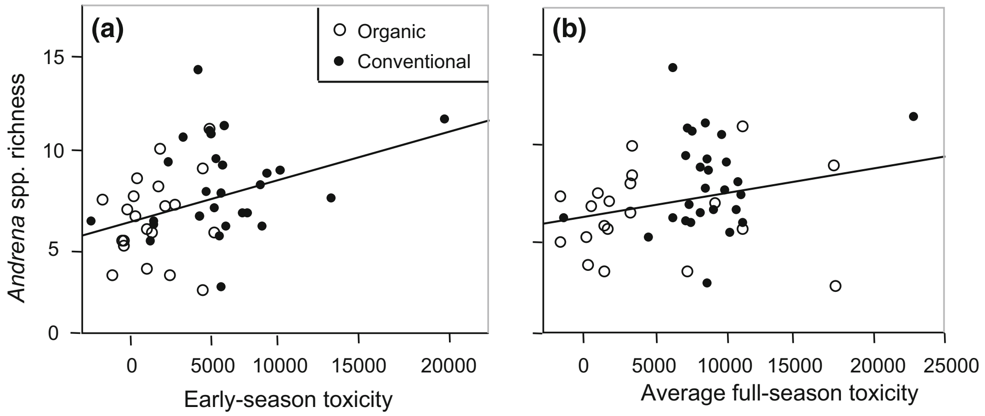

Fig. 2 Relationships between the species richness of *Andrena* spp. with **a** early-season orchard toxicity scores and **b** average full-season orchard toxicity scores. Bees were trapped within apple orchards of southern Wisconsin during apple bloom in 2010, 2012 and 2013. Partial residual regression is from the best-fit model ($\Delta AIC_c = 0$) for each response variable

was 266 ± 36. The combined number of workers and males produced by a colony and the average worker thorax width were positively correlated ($r = 0.44$, $P = 0.02$), while colony weight gain was positively correlated to the number of new queens produced by the colony ($r = 0.50$, $P = 0.007$).

Early-season and full-season toxicity scores were not significant predictors for either colony weight gain or the number of queens produced (Table 3a, b). Only year was included as a predictor variable in competing models, and the overall best-fit models did not include any of our measured variables (Tables 3a, b, 4a, b). However, both early-season and full-season toxicity scores, along with year, were significant predictors for the number of workers and males produced by bumble bee colonies (Table 3a, b). The combined number of workers and males were negatively correlated to both early-season and full-season toxicity scores in the overall best-fit models (Table 4a, b; Fig. 3a, b). Furthermore, early-season and full-season toxicity scores were significant predictors of worker thorax width, along with year and percent agriculture (Table 3a, b). There was a negative effect of early-season toxicity scores on worker thorax width in the overall best-fit model (Table 4a, b).

Discussion

Pesticides are often implicated in the declining populations of both managed bees and wild bees, particularly in regions where agricultural intensification has occurred (National Research Council 2007; Colla and Packer 2008; Potts et al. 2010; Burkle et al. 2013). In this three-year study, we did

Table 3 Model selection statistics for $i = 7$ models predicting the performance of bumble bee colonies deployed in apple orchards of southern Wisconsin (colony weight gain, the number of queens produced, the combined number of workers and males produced, and worker thorax width) as a function of year, 2012 or 2013, (*Yr*), percent agriculture surrounding the orchard at a 1 km radius (*Ag*), and orchard toxicity scores (*Tox*) calculated as (a) early-season toxicity scores including all pesticide sprays from the beginning of the year through apple bloom and (b) full-season toxicity scores including all pesticide sprays applied when bumble bee colonies were deployed in orchards, approximately March–August, of each year

i	Explanatory variables	Sqrt weight gain		Log queens		Sqrt workers/males		Thorax width	
		ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
(a) Early-season toxicity scores									
0	Intercept	**0.0**	**0.43**	**0.0**	**0.40**	2.4	0.08	42.8	0.00
1	*Yr*	**1.7**	**0.18**	**1.9**	**0.16**	**0.9**	**0.17**	**0.0**	**0.49**
2	*Tox*	2.4	0.13	2.9	0.13	**0.0**	**0.26**	42.8	0.00
3	*Ag*	2.5	0.12	2.1	0.14	3.9	0.04	45.0	0.00
4	*Tox + Yr*	4.5	0.05	4.1	0.05	**0.0**	**0.26**	**1.4**	**0.24**
5	*Tox + Ag*	5.1	0.03	4.2	0.05	2.7	0.07	45.6	0.00
6	*Ag + Yr*	4.5	0.05	4.2	0.05	2.7	0.07	**1.7**	**0.21**
7	*Tox + Ag + Yr*	7.5	0.01	6.1	0.02	2.9	0.06	4.0	0.07
(b) Full-season toxicity scores									
0	Intercept	**0.0**	**0.42**	**0.0**	**0.41**	3.3	0.06	43.9	0.00
1	*Yr*	**1.7**	**0.18**	**1.9**	**0.16**	**1.8**	**0.14**	**1.2**	**0.27**
2	*Tox*	2.2	0.14	2.4	0.12	**0.0**	**0.33**	40.9	0.00
3	*Ag*	2.5	0.12	2.1	0.15	4.9	0.03	46.2	0.00
4	*Tox + Yr*	4.4	0.05	4.1	0.05	**0.7**	**0.23**	**0.0**	**0.49**
5	*Tox + Ag*	4.9	0.04	4.4	0.04	2.6	0.09	43.7	0.00
6	*Ag + Yr*	4.5	0.04	4.2	0.05	3.6	0.06	2.9	0.12
7	*Tox + Ag + Yr*	7.4	0.01	6.3	0.02	3.5	0.06	2.7	0.13

For each response variable, competing models ($\Delta AIC_c < 2$) are bolded

Table 4 Parameter estimates (β ± SE) from the best-fit models ($\Delta AIC_c = 0$) explaining the performance of bumble bee colonies deployed within apple orchards of southern Wisconsin (colony weight gain, number of queens produced, combined number of workers and males produced, and worker thorax width)

Explanatory variable	Sqrt weight gain	Log queens	Sqrt workers/males	Thorax width
(a) Early-season toxicity				
Intercept	9.9 ± 1.1	1.7 ± 0.3	17.9 ± 1.5	1.6 ± 0.15 ($\times 10^3$)
Tox			−6.8 ± 3.0 ($\times 10^{-4}$)	
Yr (2013)				−0.8 ± 0.1
Ag				
(b) Average full-season toxicity				
Intercept	9.9 ± 1.1	1.7 ± 0.3	18.7 ± 1.6	1.5 ± 0.15 ($\times 10^3$)
Tox			–4.6 ± 1.9 ($\times 10^{-4}$)	−1.4 ± 0.7 ($\times 10^{-5}$)
Yr (2013)				−0.8 ± 0.1
Ag				

Explanatory variables include year, 2012 and 2013, (*Yr*), percent agriculture at a 1 km radius surrounding the orchard (*Ag*), and orchard toxicity scores (*Tox*), calculated as (a) early-season toxicity scores including all pesticide sprays from the beginning of the year through apple bloom and (b) full-season toxicity scores including all pesticide sprays applied when bumble bee colonies were deployed in orchards, approximately March–August, of each year

not find the expected negative relationship between pesticide toxicity scores and overall wild bee abundance or species richness during crop bloom. However, one subset of the wild bee community, *Lasioglossum* spp., was less abundant and species rich at orchards with high toxicity scores. Additionally, sentinel colonies of bumble bees produced fewer and smaller workers within orchards that had high toxicity scores. Thus, the effects of pesticides appear to vary among taxa and with associated life-history traits that increase bee sensitivity or exposure to on-farm pesticide use.

Toxicity scores

Our calculated toxicity scores incorporated three important factors that could determine the effects of pesticides on bees: the acute toxicity of the pesticide (based on its honey bee LD_{50}), the residual activity of the pesticide, and the

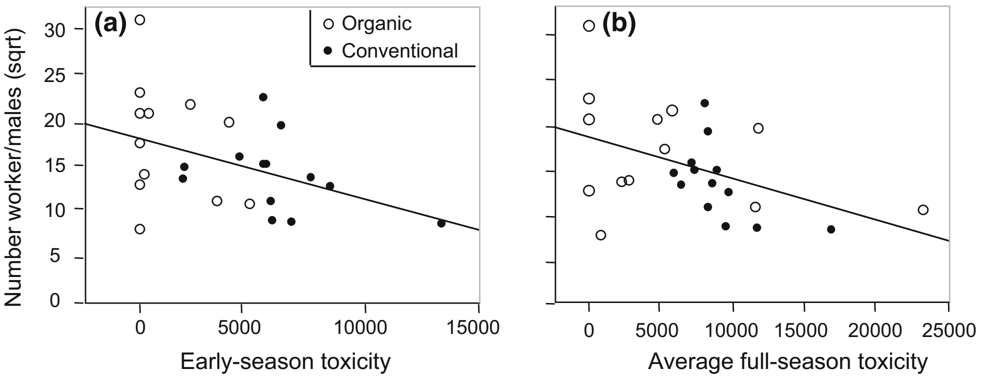

Fig. 3 Relationships between the combined number of workers and males produced by bumble bee colonies deployed within apple orchards of southern Wisconsin in 2012 and 2013 and **a** early-season orchard toxicity scores and **b** full-season orchard toxicity scores. Partial residual regression is from the best-fit model ($\Delta AIC_c = 0$) for each response variable

amount of pesticide applied within the orchard. However, additional factors may influence bee exposure to pesticides, such as the weather and presence of flowers during application, which could not be accounted for in our calculations. Additionally, our toxicity scores assume that the effects of multiple pesticide applications are additive, and therefore do not take into account potential synergistic relationships or non-linear effects on bees. While we recognize the limitations of these scores, they are useful for comparing orchards that differ greatly in pesticide use, offering a more nuanced alternative to categorical management (e.g. conventional and organic). In our study, toxicity scores showed significant variation within and between organic and conventional orchards, with some organic orchards having higher toxicity scores than conventional orchards due to numerous pesticide applications, high application rates, and the use of relatively toxic organic insecticides such as spinosad and mineral oil. Therefore, a continuous index of pesticide-use intensity may better explain variability in bees across orchards with different pest management programs.

The two calculated toxicity scores, early-season and full-season, were strongly correlated to one another, suggesting that farmers' relative pesticide-use intensity is consistent throughout the growing season. Furthermore, wild bee and bumble bee responses were similar to both toxicity scores, indicating that the scores are comparable in their ability to predict wild bee abundance and richness, or bumble bee colony performance. Early-season toxicity scores included mainly fungicides applied before apple bloom, and were expected to have immediate, within-year, negative effects on wild bee activity. Full-season toxicity scores additionally included insecticides, and a few fungicides, applied after bloom, which could affect wild bees with long foraging periods and bumble bee colonies active throughout the summer. Interestingly, orchards' full-season toxicity scores were relatively consistent across two consecutive years despite yearly variability in weather, crop size, and pest pressure, suggesting an overall consistent pest management philosophy for an orchard. We thus expected that patterns of wild bee abundance and species richness during crop bloom would be related to average full-season toxicity scores due not only to pesticides applied during our study period, but to legacy effects from similar management practices in recent past years.

Wild bee abundance and diversity across a gradient of toxicity scores

Contrary to our expectations, orchards applying highly toxic insecticides did not have reduced overall wild bee abundance or species richness during crop bloom relative to orchards with lower toxicity management. This overall pattern was due in part to opposing responses by the dominant bee genera *Andrena* and *Lasioglossum*; while *Lasioglossum* spp. were negatively affected by toxicity scores, *Andrena* spp. were positively affected. The positive response of *Andrena* spp. to toxicity scores is difficult to explain, but it is possible that orchard toxicity scores were correlated with some other beneficial aspect of orchard management, or with resource availability within the orchard. In particular, orchards with higher toxicity scores may have had a denser display of apple flowers, which could lead to a higher abundance and richness of *Andrena* spp. during bloom. Additionally, the life-history traits of *Andrena* spp. could explain the lack of a negative response to toxicity. *Andrena* spp. are primarily springtime foragers with relatively short foraging periods, and are thus not exposed to pesticides applied after apple bloom and included in full-season scores (Michener 1974, 2000). And while their foraging periods may better overlap with early-season scores, exposure to such early-season sprays will depend on foraging or nesting location. As many *Andrena* spp. in orchards were medium-large bodied bees in the subgenus *Melandrena*, with associated long foraging ranges (Greenleaf et al. 2007), they could have been foraging in habitats adjacent to orchards before apple bloom and therefore exposed to very few orchard pesticides. Furthermore, for species that can move across habitats, within-orchard pesticide applications may not appear to influence local activity if regional bee populations can recolonize the orchard after a mortality event from a pesticide application. In this scenario, factors at the landscape scale affecting the source pool of wild bees may affect local bee activity as much or more than within-orchard pesticide use. And indeed, we found that the percentage of agriculture in the surrounding landscape had a negative effect on both *Andrena* abundance and species richness during apple bloom.

On the other hand, many life-history traits shared by *Lasioglossum* spp. could increase their exposure and sensitivity to orchard pesticides and explain their negative response to toxicity scores. First, many *Lasioglossum* species are social, a trait that is expected to increase sensitivity to pesticides particularly if they are applied early in the season during queen activity and colony formation (Michener 1974, 2000; Williams et al. 2010; Brittain and Potts 2011). Additionally, *Lasioglossum* spp. generally have longer foraging periods as compared to *Andrena* spp., thereby increasing their exposure to season-long pesticide applications (Michener 1974, 2000). And finally, the majority of *Lasioglossum* spp. in our study system are small-bodied bees in the subgenus *Dialictus*, and therefore more likely to have short foraging ranges (Michener 1974; Greenleaf et al. 2007; Gibbs 2011). We thus expect their populations to be strongly regulated by local factors including orchard management rather than broad-scale landscape factors. The activity of small-bodied bees within the orchard during bloom is also unlikely to be influenced by foragers from the surrounding landscape due to the limited foraging ranges of these bees. Small-bodied bees may furthermore show a stronger response to toxicity scores because their small body size results in increased sensitivity to smaller doses of pesticides (Thompson and Hunt 1999; Malone et al. 2000).

Bumble bee colony performance across a gradient of toxicity scores

Though pesticide use did not affect all measured bumble bee colony performance traits, including the number of new queens (gynes), there were negative effects on the production of workers and males, and on worker body size. These results are consistent with other studies that examined bumble bee responses to specific pyrethroid and neonicotinoid insecticides and found that the number of workers, but not gynes, was negatively affected (Gels et al. 2002; Gill et al. 2012; Baron et al. 2014; but see Whitehorn et al. 2012). While the number or size of workers may not directly contribute to bumble bee population growth rates, as only queens reproduce, workers could have an indirect effect on population growth via their effects on colony and gyne health. The negative effects of orchard pesticides on bumble bees may be due to bumble bee life-history traits, or due to our ability to detect effects at the individual bee and colony level that are harder to detect at the bee community level. Like many of the *Lasioglossum* spp., bumble bees are social and have long foraging periods, factors that could increase their sensitivity and exposure to both early-season and season-long pesticide applications (Michener 2000; Brittain and Potts 2011). Unlike small sweat bees, however, large-bodied bumble bees have long foraging ranges that would enable them to forage outside of the orchard (Osborne et al. 1999). But, our placement of colonies within the center of orchards guaranteed that the bees were nesting within orchards and likely ensured some exposure to orchard pesticides throughout the season. Our results suggest that highly toxic pesticides can decrease colony growth and worker size, with potential consequences for local populations of wild bumble bees.

Conclusions and implications

Farmers of pollinator-dependent crops are concerned with how their pest management practices affect bee activity during crop bloom, as this may have deleterious effects on crop pollination. In this study, we found that total wild bee abundance and species richness during apple bloom were not significantly related to orchard toxicity scores due to differing responses by common bee genera. These findings do not necessarily suggest that orchard pesticide applications are benign, or even beneficial, to bees, but rather illustrate that different taxa have variable exposure and sensitivity to on-farm pesticide applications. Bees that did show negative responses to toxicity scores, including *Lasioglossum* spp. and sentinel bumble bees, shared certain life-history traits expected to increase their vulnerability to pesticides including long foraging periods and sociality. Our results highlight the need to examine pest management on a continuous gradient, as there was overlap in toxicity scores between organic and conventional categories, and suggest that studies should examine species or taxon-specific responses in addition to overall, community-wide responses.

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