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Negative effects of pesticides on wild bee communities can be buffered by landscape context

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Wild bee communities provide underappreciated but critical agricultural pollination services. Given predicted global shortages in pollination services, managing agroecosystems to support thriving wild bee communities is, therefore, central to ensuring sustainable food production. Benefits of natural (including semi-natural) habitat for wild bee abundance and diversity on farms are well documented. By contrast, few studies have examined toxicity of pesticides on wild bees, let alone effects of farm-level pesticide exposure on entire bee communities. Whether beneficial natural areas could mediate effects of harmful pesticides on wild bees is also unknown. Here, we assess the effect of conventional pesticide use on the wild bee community visiting apple (*Malus domestica*) within a gradient of percentage natural area in the landscape. Wild bee community abundance and species richness decreased linearly with increasing pesticide use in orchards one year after application; however, pesticide effects on wild bees were buffered by increasing proportion of natural habitat in the surrounding landscape. A significant contribution of fungicides to observed pesticide effects suggests deleterious properties of a class of pesticides that was, until recently, considered benign to bees. Our results demonstrate extended benefits of natural areas for wild pollinators and highlight the importance of considering the landscape context when weighing up the costs of pest management on crop pollination services.

1. Introduction

Thirty-five per cent of global food production, including our most nutrient-rich crops, benefits from insect pollinators, primarily bees [1,2]. Although more than 20 000 valid bee species have been described [3], pollination management in modern agriculture traditionally involves a single species, the European honeybee, *Apis mellifera* L. However, steady declines in honeybee populations over the past 50 years [4], and significant colony losses owing to ‘Colony Collapse Disorder’ [5,6], have resulted in costly hive rental fees and supply shortages for growers in North America. Relying on a single pollinator species for food production is not only risky [7], it is inefficient: for many crops, successful pollination consistently increases with wild bee but not honeybee abundance [8]. This suggests that wild bees may compensate for continued honeybee losses, but honeybees cannot replace wild bees [9]. Abundance and diversity of bee communities drive pollination services, with abundance influencing the level of pollination provided to the crop [8], and diversity stabilizing pollination services through time and space [10–12]. Strategies for sustainable food production must, therefore, include schemes to manage agricultural landscapes in a manner that supports both wild bee abundance and diversity [8].

Agronomic practices have intensified dramatically within the past century, trading diverse small farms for large monocultures and increasing use of

agrichemicals [13]. The risks to wild bees associated with habitat loss owing to agricultural intensification are well established [14–18]. By contrast, we know little about the response of wild bee communities to farm-level pesticide exposure within agroecosystems. Mass die-offs of wild bees inadvertently exposed to insecticides [19] demonstrate acute, lethal effects of pesticides at population and community levels. Similarly, laboratory and field toxicity tests on managed bees show that even sublethal effects of pesticides on individual bees can have ramifications for bee populations and communities [20–25]. Laboratory toxicity tests on individual wild bees have rarely been conducted (but see [26,27]). Wild bee communities comprise a diverse assemblage of species varying in size, life history and foraging strategy, all of which influence exposure probability and susceptibility to pesticides [20,28]. With over 100 pesticide residues found in honeybees and hives [29], the number of pesticides to which wild bees are exposed, as well as unknown possible synergistic effects, make predicting the community response to pesticides based on individual laboratory tests untenable. While field comparisons of organic and conventional farms have been the first to reveal measurable effects of increasing pesticide use on wild bee communities [18], differences in other farm management practices, such as weed control, crop rotation and tilling impacts, make it difficult to attribute differences in bee communities to pesticide use *per se*. Moreover, because organic farming represents less than 1% of US and global agriculture [30], such categorical comparisons leave us with a large gap in documenting the range of effects within conventional spray regimes. Field-level studies addressing the combined effect of pesticides across a continuum of realistic conventional exposure rates on bee communities are urgently needed.

Both loss of natural (here, defined as both natural and semi-natural) areas in the landscape and increased agrichemical use may negatively affect wild pollinators and their services, yet little is known about their potential interactions. Natural areas provide food and nesting resources for pollinator communities leading to increased crop pollination services [10]. While these services have been shown to diminish as farming practices intensify [18], no one has yet explicitly examined whether natural areas mitigate effects of pesticides on wild pollinator communities. If natural areas provide a large enough pool of wild pollinators that visit a crop field or provide refuge from pesticides, they could theoretically buffer harmful effects of pesticides. Understanding whether the impact of pesticides depends on the landscape context would inform accurate predictions and decision-making regarding the management of our agricultural landscapes. Here, we use natural gradients of both conventional pesticide use and percentage of natural areas within the surrounding landscape to investigate (i) the effect of pesticides on wild bee communities visiting apple (*Malus domestica*), an economically important crop, and (ii) dependence of pesticide effects on the landscape context.

2. Material and methods

(a) Bee sampling

We surveyed a total of 19 orchards for abundance and species richness of bees visiting apple blossoms (16 in 2011 and 19 in 2012). A key feature of this study is that these orchards were situated within two independent ($r = 0.14$, $p > 0.05$) gradients

of conventional pesticide use and amount of surrounding natural habitat (see electronic supplementary material, figure S1). Bees visiting apple were net-collected along 15-min, standardized transects one to two times during bloom (see electronic supplementary material, Material and methods, for methodological details). Surveys were conducted between 10.00 and 15.30 on days with temperature above 16°C and with enough sun to cast a shadow. Foraging distances for solitary bees, the dominant bee fauna in our study orchards, are typically less than 1.5 km [31,32]. To ensure independence of sites, we only used orchards that were spatially separated by a distance greater than this typical foraging range (minimum distance between sites 1.9 km). Percentage of open flowers in the orchard and temperature were recorded with each survey (see electronic supplementary material, Material and methods, for methodological details). We also recorded density of honeybee hives at each site as they are commonly rented for pollination.

(b) Natural habitat

In this study, we broadly defined ‘natural’ habitat as land that was minimally managed and not cultivated for arable crops. Specifically, natural habitat included forests, wooded and herbaceous wetlands, shrublands and grasslands (see electronic supplementary material, table S1). While natural components of the landscape surrounding orchards were dominated by deciduous forest, nearby agricultural areas were dominated by annual row crops, pasture or fallow fields and apple orchards. We used a geographical information system (GIS) ArcGIS v. 10 [33] to quantify percentage of natural habitat surrounding each orchard at various spatial scales from the Cropland Data Layer ([34] 30 m resolution), provided by USDA NASS. Owing to CDL’s low accuracy in detecting orchards, we merged the CDL with a hand-digitized layer of apple orchards created from National Agricultural Imagery Program county-level, digital ortho-photos zoomed at 1 : 2000 ([35]; 1 m resolution). Land cover was consolidated from a set of over 100 predefined categories to 17 land cover classes, which were further consolidated into natural habitat, agriculture and developed land use. We quantified spatial extent of natural habitat within five GIS buffer radii (300, 500, 1000, 1500 and 2000 m) centred on study orchards. We determined that 2 km was the scale at which percentage natural area in the landscape provided the best model fit (see electronic supplementary material, Material and methods, for methodological details) and conducted all analyses with landscape data at this scale.

(c) Pesticide use intensity

Spray records from the entire 2011 growing season were collected from participating growers. To quantify spray intensity across orchards, which use different compounds at varied rates and schedules, we modified the environmental impact quotient (EIQ) Field Use Rating [36] to develop an index of pesticide use intensity (PUI) based on known impacts to bees. The EIQ Field Use Rating quantifies the seasonal cumulative environmental impact of a field’s spray regime, taking account of both pesticide toxicity and exposure to risk, and has been found to be a reliable indicator of environmental impacts [37]. Each pesticide has an assigned EIQ value (last updated in 2010), a cumulative measure of predicted impacts to human, wildlife, beneficial insect, soil and water health [36]. Toxicity of a pesticide to honeybees falls under impacts to beneficial insects and is referred to here as the bee impact quotient (BIQ). The BIQ is a product of a pesticide’s scaled toxicity (1 = low, 3 = medium, 5 = high) to honeybees [38] and its plant surface half-life (see electronic supplementary material, table S2, for study-wide list of pesticides used and BIQs). Our PUI provides a per-acre calculation of the cumulative effect of a given orchard’s spray regime on bees; as such, it accounts for differences in orchard size. Each study site’s PUI was quantified

by summing, across all pesticides used on apple within the orchard, the product of a pesticide's (i) BIQ, (ii) percentage active ingredient in material sprayed and (iii) application rate (quantity per acre, equation (2.1)) [36].

$$\text{Pesticide use index} = \sum_{i=1}^n \text{BIQ}_i \times \% \text{ active ingredient}_i \times \text{application rate}_i. \quad (2.1)$$

In addition to calculating an overall pesticide use index for the entire 2011 growing season, we examined whether compound class (i.e. fungicide versus insecticide) and timing were important predictors of pesticide effects on bees. We subdivided overall spray data according to (i) three time periods: before, during and after apple bloom; and (ii) three class categories: fungicide, insecticide and plant growth regulators (PGRs). Bactericides and acaricides were included in fungicide and insecticide categories, respectively. We conservatively defined bloom sprays to fall within a five-week period around the bloom, starting one week before and ending four weeks after the first day of bloom. We derived first day of bloom from our observations of floral phenology during bee surveys and from consulting with growers. Reasons for extending our definition of bloom by a week on either end include: (i) bees have been observed to visit un-opened blossoms in the balloon stage, (ii) bees visit old flowers that have lost their petals but still supply nectar, (iii) late blossoms can be found weeks after peak bloom, and (iv) our estimates of early bloom are accurate within 2–3 days (M.G.P. 2011, personal observation).

BIQ values were unavailable for inert ingredients commonly added to spray solutions in order to enhance the performance of pesticide applications, such as surfactants and adjuvants, in spite of their recently demonstrated sublethal toxicity to bees [39]; nor were BIQs available for fertilizers or several PGRs used for thinning. We assumed that fertilizers are generally not toxic to bees and did not include them. Only one PGR, Prohexadione Calcium, has an assigned BIQ, which was used for all PGRs applied in study orchards. Of 19 surveyed, two orchards applied petroleum oil early in the growing season to control overwintering mites and scales. With one of the highest application rates (5–8 kg ha⁻¹) and relatively high BIQ (18.1), the single application of oil at the two study orchards increased overall pesticide use indices by 22 and 54%. We conducted linear models with and without oils and the results showed similar effects. We therefore chose to present the models excluding the oils because these best fitted the assumption of homoscedasticity.

(d) Statistical analyses

To test the impacts of conventional pesticide use and percentage of natural area on pollinating bee communities, we ran three initial general linear mixed models (GLMM) with the response variables wild bee abundance, wild bee species richness and honeybee abundance. In each GLMM, we included the following fixed effects: percentage natural area (within a 2 km radius), PUI, year, orchard bloom display, local orchard diversity, hive density, temperature, as well as all three- and two-way interactions among natural area, PUI and year. Because wild bee communities are known to fluctuate naturally year-to-year [40], we included year in the model and interaction terms. Significant interactions between natural area and pesticide use would indicate a landscape-dependent response of bees to pesticide exposure. Percentage natural area and pesticide use index were centred on the mean and temperature was log-transformed. To tease apart the effect of pesticides, *per se*, from other differences in orchard management, we included a categorical covariate of within-orchard diversity based on orchard size and crop diversity [18]. Locally diverse orchards included (i) orchards only growing

apple but smaller than 10 ha, and (ii) orchards growing additional fruit crops but smaller than 20 ha. All orchards with contiguous areas larger than 20 ha were categorized as locally simple. To account for a blocking effect of three geographical regions in which sites were largely clustered (see electronic supplementary material, Material and methods, for methodological details), we included region as a random variable. Orchard was also included as a random factor, nested within region, to account for repeat visits within a sampling season. A PUI × year term was added to test a potential lag response of bees to pesticide use. We used stepwise deletion to simplify models (where $p > 0.05$). Starting with interaction terms, the explanatory variable with the highest p -value was removed. We then tested for loss of explanatory power resulting from variable removal, by comparing models with and without the variable using analysis of variance (maximum-likelihood fitting). If models did not differ significantly ($p > 0.05$), the explanatory variable was removed. We used maximum-likelihood estimation during the deletion process and to report ΔAIC between final and null models, but fitted final models using restricted maximum likelihood to provide unbiased model estimates [41]. We ran analyses on wild social and solitary bees separately in order to determine whether social behaviour altered the response to pesticide use.

In order to differentiate pesticide effects owing to insecticides and fungicides and the timing of their application, pesticide use indices attributed to each chemical class (i.e. a fungicide use index [FUI] and an insecticide use index [IUI]) within each of the three time periods (before, during or after bloom) were recalculated per orchard. Visual assessment of insecticide use after bloom revealed a potentially disproportionate contribution of Phosmet to the insecticide index, causing three orchards to be outliers and reducing model fit ($\Delta\text{AIC} = 14$). Phosmet is considered a highly toxic organophosphate, with the maximum BIQ (28.5) observed within our study. Across seven orchards, where it was applied once after bloom (see electronic supplementary materials, table S2, for application rates), Phosmet contributed 42–87% of an orchard's post-bloom insecticide index value. Although several other insecticides had equally high BIQ, Phosmet's application rate (1 kg ha⁻¹ or more) exceeded others by three or more fold. While one of the PUI's strengths is to account for both toxicity and dose, the EIQ field use rating upon which the PUI was based has been found to bias impact ratings of pesticides with high application rates, notably when differences in toxicity are not captured by the categorical hazard rating [42,43]. High application rates for Phosmet compared with similarly rated pesticides in our study (e.g. Indoxacarb, Thiamethoxam and Imidacloprid) suggest that this may very well be the case for Phosmet. We therefore recalculated post-bloom insecticide indices, as well as total PUI, for all orchards without Phosmet. We chose to present total PUI results without Phosmet because its removal did not change our results (except for the post-bloom analyses where we have presented results with and without Phosmet in the electronic supplementary material, table S5). To test whether we missed an important influence on bee communities by excluding this compound, we included a categorical Phosmet factor. Where final GLMM models for total wild bee abundance and species richness included a significant effect of PUI, we reran final models with fungicide and insecticide use indices treated separately in place of the original combined PUI, including new interaction terms with percentage of natural area. The effects of fungicide and insecticide use indices were compared within a single time period, resulting in three parallel models for each bee response variable. We proceeded with stepwise deletion as described above. For all models, the fixed effect of our dummy Phosmet variable was not significant.

All GLMMs used a normal distribution after response variables were $\ln(y + 1)$ transformed. We verified that data met assumptions of normality and homoscedasticity. We used a Poisson distributed,

zero inflated generalized linear mixed model (ZIGLMM) to investigate the social bee response owing to many zeros and non-normal distribution of the data [44]. We analysed data with and without male bees (10% of total bees) and found that excluding males improved model fit but did not change overall results. We therefore present analyses without males. Sample independence was verified by visually assessing GLMM residuals for spatial autocorrelation, using sample variograms [45]. For all analyses, we verified that predictor variables in full models were not collinear (variance inflation factor (VIF) less than 10); VIF was consistently less than 2 [46]. All statistical analyses were conducted using R [47]; we employed the 'nlme' package [48] for GLMM and the 'glmmADMB' package [49,50] for ZIGLMM analyses.

3. Results

(a) Apple-visiting bee communities

In 2011 and 2012, we conducted a total of 320 standardized transects across 16 and 19 orchards, respectively, for 80 h of active net-collecting of bees visiting open apple blossoms. We surveyed a total of 1820 honeybees and 3800 wild bees, comprising 71 species. Of the 3800 wild bees collected, the majority (3418) were females, representing 68 species (see electronic supplementary material, table S3, for species list). The wild bee community was numerically and taxonomically dominated by solitary, ground-nesting *Andrena*, commonly known as mining bees (1076 individuals, 24 species). Eight *Bombus* species made up 6% of wild bees collected and were primarily gynes, with *Bombus impatiens* Cresson comprising 75% of bumblebee individuals collected.

(b) Effects of landscape context and orchard pesticide use

Honeybee abundance was driven by temperature alone ($t_{46} = 2.43$, $p = 0.02$; see electronic supplementary material, table S4, for full statistics), while wild bee communities were driven by year, temperature, characteristics of the landscape and orchard management. Wild bee abundance and species richness increased with percentage of natural area in the surrounding landscape across years (abundance: $t_{13} = 4.41$, $p < 0.001$; richness: $t_{13} = 5.58$, $p = 0.001$, figure 1). Both solitary (abundance: $t_{13} = 3.11$, $p = 0.008$; richness: $t_{13} = 3.74$, $p = 0.003$; electronic supplementary material, figure S2) and social (abundance: $z = 4.96$, $p < 0.001$; richness: $z = 3.69$, $p < 0.001$; electronic supplementary material, figure S2) bees showed positive relationships with the percentage of natural area.

Wild bee abundance decreased significantly with increasing pesticide use 1 year after application (PUI \times year: $t_{40} = -2.27$, $p = 0.03$; figure 2), while wild bee species richness decreased marginally across years (PUI: $t_{13} = -2.04$, $p = 0.06$). While having no measurable effect on social bees, increased pesticide use was associated with decreased solitary abundance and species richness 1 year after application (PUI \times year, abundance: $t_{40} = -3.12$, $p = 0.003$; richness: $t_{40} = -2.43$, $p = 0.02$; electronic supplementary material, figure S3). Overall, 2011 pesticide effects on wild bee abundance in 2012 were driven by fungicides applied before the bloom (abundance, FUI: $t_{15} = -2.99$, $p = 0.009$; richness, % natural habitat \times FUI: $t_{13} = -3.00$, $p = 0.01$; see electronic supplementary material, table S5, for full statistics; figure 2*b,f*) and insecticides (Phosmet excluded) applied after bloom (abundance, IUI: $t_{15} = -4.48$, $p < 0.001$; richness, IUI: $t_{15} = -3.85$, $p = 0.0016$; figure 2*d,h*).

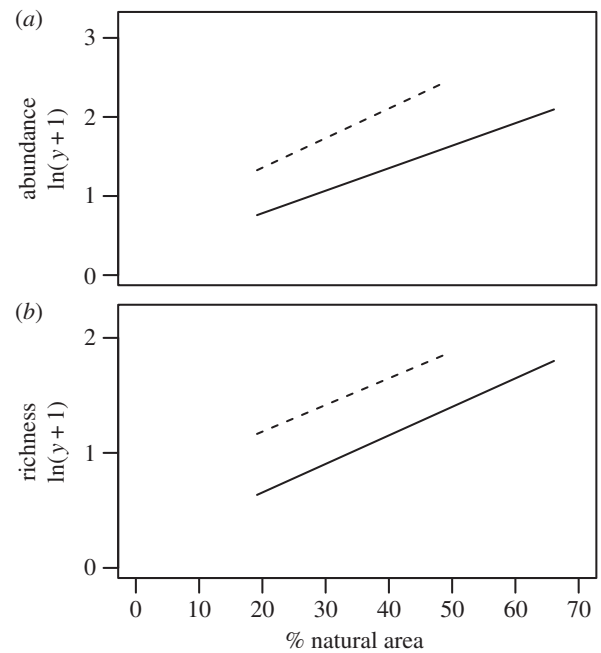


Figure 1. Bivariate relationships between surrounding natural habitat (2 km scale) and average wild bee (a) abundance and (b) species richness per transect in apple orchards in 2011 (dotted lines; $N = 16$) and 2012 (solid lines; $N = 19$). Percentage of natural area had a significant positive effect on wild bee abundance and species richness across years. Data are fitted values derived from final GLMMs, with temperature held constant at 21°C, and span the observed range of natural area for the given years.

Susceptibility of wild bee communities to pesticides applied in 2011 depended on the amount of natural area in the surrounding landscape (% natural habitat \times PUI, abundance: $t_{13} = 2.89$, $p = 0.01$; richness: $t_{13} = 2.90$, $p = 0.01$; figure 3). As natural habitat within the surrounding landscape increased, the negative relationship between pesticides and wild bee abundance and species richness weakened. This pattern was driven by the dominant solitary bee response (% natural habitat \times PUI, abundance: $t_{13} = 3.06$, $p = 0.009$; richness: $t_{13} = 3.03$, $p = 0.02$; figure 3), as we observed no such interaction for social bee abundance or species richness.

4. Discussion

Through habitat loss and increased use of conventional agrichemicals, global expansion of intensified agricultural practices threatens vital ecosystem services, including pollination by wild bees [1,51]. Agroecosystems that balance benefits of pest management with costs incurred to wild pollination services are needed [52], but their design is hampered by our limited understanding of how agrichemicals affect wild bee communities in crop fields in varying landscape contexts. Here, we provide novel correlative evidence that the risk from increasing pesticide use to the abundance and diversity of wild bee communities in orchards is buffered by the presence of natural habitat.

Surrounding natural areas, largely mixed deciduous forest, were a source of wild bee pollinators in upstate New York orchards. Both abundance and diversity of wild pollinator communities visiting apple in Wisconsin [53] and crop systems around the world [18] have been shown to benefit from greater amounts of natural area in the landscape. Extensive natural areas provide increased nesting and foraging opportunities,

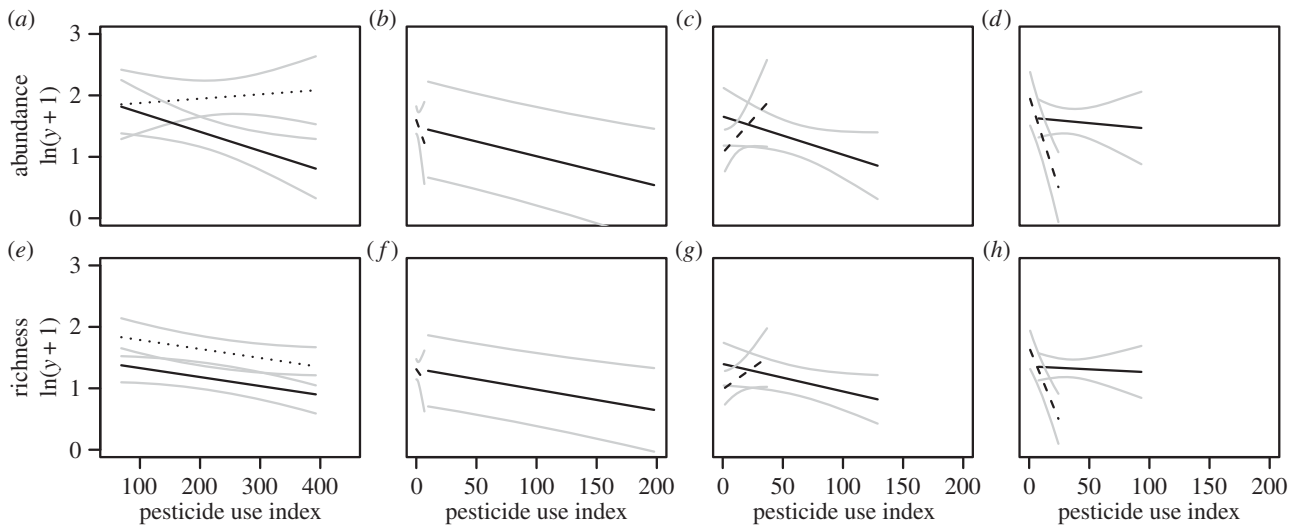


Figure 2. Bivariate relationships between intensity of conventional pesticide use (PUI) in 2011 and wild bee abundance (a) and species richness (e) per transect in orchards in 2011 (dotted lines) and 2012 (solid lines). PUI in 2011 had significant negative effects on wild bee species richness in both years and on abundance in 2012. Relationships between 2011 PUI and 2012 wild bee abundance (b,c,d) and species richness (f,g,h) are further separated by insecticides (dashed lines) and fungicides (solid lines) over three time periods relative to bloom: before (b,f), during (c,g) and after (d,h). Grey lines represent 95% CIs. Data are fitted values derived from final GLMMs with main effects of overall pesticide use, insecticide and fungicide use intensity included for visual representation if removed from final models; temperature and centred percentage of natural area were held constant at 21°C and 0%. Only fungicides and insecticides applied before and after bloom, respectively, showed significant ($p < 0.01$) negative associations with wild bee abundance and richness.

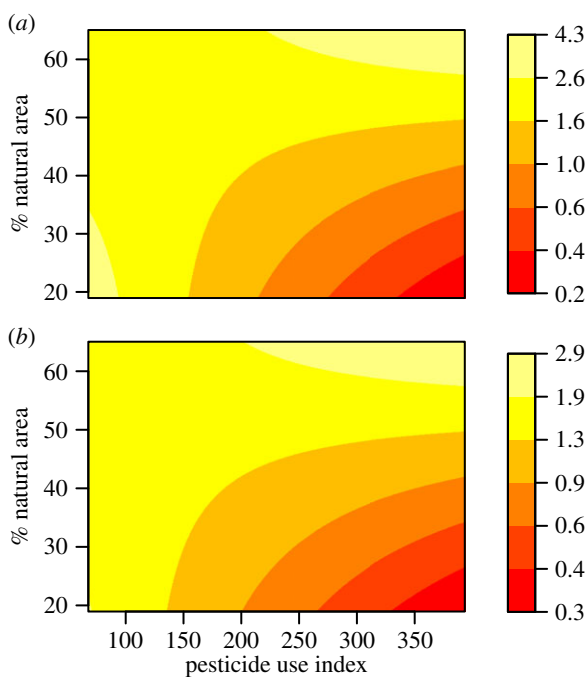


Figure 3. Heat maps of interactions between natural habitat surrounding orchards (% natural area at 2 km radius) and intensity of conventional pesticide use (pesticide use index) in 2011 on wild bee abundance (a) and species richness (b) per transect in 2012. As percentage of natural areas surrounding orchards increased, the negative relationship between increasing pesticide use and wild bees weakened. Data are fitted values derived from final GLMMs, with temperature held constant at 21°C. Light yellow indicates highest and deep red indicates lowest wild bee abundance and species richness. Axes represent the ranges of percentage natural habitat and PUI observed in the study.

allowing for greater population sizes and species richness [54]. As bees are highly mobile organisms [10] and apple is an attractive mass resource, community abundance and richness of wild bees in orchards were influenced by the regional

landscape (a 2 km scale) and not necessarily the habitat immediately adjacent to the orchards.

Our approach of using an index to capture additive toxicity of pesticide programmes across orchards in a standardized manner is a flexible and effective method of characterizing spray intensity. While ours is the first to look at the combined effects of all pesticides applied, investigation of insecticide impacts on wild pollinators of Michigan blueberry with a similar index also found a linear, negative response of the bee community that was strongest the following year [55]. Field studies focused on a single or select toxic insecticide(s) might miss important effects from heavily used pesticides considered to have low toxicity, like fungicides, or from synergies among compounds [56,57]. Such continuous and additive effects of pesticides are not measurable in categorical comparisons (e.g. organic versus conventional). Moreover, while categorical comparisons have been the first to demonstrate a response of wild pollinators to varying intensities of pest management [18], one must account for important differences in farm management, such as crop rotation and weed management, to associate dissimilarities in bee communities between organic and conventional orchards to pesticide regime, *per se*. As an index that simplifies the impact of an orchard's spray regime on bees to a single number, the PUI had some limitations. For example, materials applied at exceptionally high rates (kg ha^{-1}), such as oil and Phosmet, seemed to inflate orchard PUI in our study. A PUI that does not accurately reflect pesticide risk to wild bees in the field may result from divergent sensitivities between wild bees and honeybees; however, in the case of Phosmet, at least, field exposure to Phosmet has been shown to produce similar mortality effects on honeybees and two solitary bees [58]. A more plausible explanation is that the PUI's narrowing of relative toxicity to three categories can result in the assignment of BIQs that are too low or too high for some materials [42]. The product of a BIQ that is too high and an exceptionally high application rate could exaggerate the impact of a pesticide even more [43]. This index seems

most effective when the types of pesticides applied across study sites are similar, as most materials were across our orchards. Ultimately, the pesticide use index enabled us to combine continuous gradients of both conventional pesticide use and land use intensity to look at the landscape context of pesticide effects on entire bee communities.

By considering the full complement of pesticides applied in the field, our results show that intensified use of not only insecticides but also fungicides can render orchards a risky environment for wild pollinators. Similar to previous work focused solely on effects of insecticide applications on wild bees in grape [59] and blueberry [55], when we exclude Phosmet, we observed a steep negative relationship between wild bee communities and intensified use of insecticides after bloom. While the previous studies attributed this late season effect to additive sublethal exposure throughout the growing season, in our study system late in the season is simply when more insecticides are applied. The linear decline of bees suggests a dose response, meaning the risk to bees increased directly as their exposure increased. Similarly, high and repeated exposure is the most likely explanation for why fungicides, with low honeybee toxicity [58,60], had a measurable impact on wild bees. Fungicides are used to prevent the spread of fungal pathogens during rain events and were most heavily employed in early spring when precipitation is most common. Given that (i) fungicide applications are tightly linked to precipitation and (ii) heavy rainfall could foreseeably depress wild bee survival, we calculated Pearson product-moment, two-way correlations between pesticide use indices and total rainfall (10.3 ± 0.4 mm, mean ± 1 s.e.) in April and May 2011. We found no significant correlations between rainfall and pesticide use within our study (PUI: $r_{17} = -0.23$, $p = 0.3$; FUI: $r_{17} = -0.27$, $p = 0.26$; IUI: $r_{17} = 0.07$, $p = 0.8$), indicating that pesticide impacts on bee community structure are genuine and not simply an artefact of precipitation. That pre-bloom fungicide sprays had the strongest negative relationship with wild bee abundance and species richness in our study indicates that wild bee communities are visiting orchards before apple blooms. While growers limit their use of insecticides to protect pollinators, fungicides are commonly applied throughout the apple bloom because they are not labelled as dangerous to bees. Because apple provides an attractive mass bloom and likely concentrates bees from the surrounding landscape, we predicted that sprays would be especially harmful during the bloom. However, in our study, fungicide spray regimes before and insecticide use after bloom had the strongest relationships with declines in the wild bee fauna, and highlight the importance of minimizing pesticide use beyond the bloom period. Unlike honeybees that reside in orchards during bloom only and showed no response to increasing pesticide use in orchards, wild bees have a greater exposure risk to pesticides as they actively forage on floral resources located in and around orchards weeks before and after apple bloom [61].

While we provide strong correlative evidence for an impact of fungicides on wild crop pollinators, the mode of action remains unclear. The observed lag in wild solitary bee response to increasing fungicide levels suggests reduced bee fitness. Altered foraging efficiency or nest recognition could decrease offspring production, but so could increased susceptibility of larvae to pesticides if toxins made it into pollen provisions. Honeybee pollen collected from orchards sprayed with fungicides had fewer beneficial fungal species [62], indicating that

digestion of pollen masses by larvae may be altered by fungicide exposure if such mutualisms are important for non-*Apis* nutrition, as well. At present, most laboratory toxicity tests are conducted on eusocial *Apis* and *Bombus*. While our study shows that bee toxicities based on honeybees can be predictive of field effects on wild bee communities, mechanistic understanding of pesticide risk to wild bee communities requires small-scale, manipulative toxicity tests on solitary bee species [27,63]. The few such studies on solitary bees reveal that some fungicides can be acutely and chronically toxic to solitary mason bees (*Osmia lignaria* Say) [25,64] and supports species-specific toxic thresholds among bees. Fungicides alone may have low toxicity, but they may interact with other pesticides or with 'inactive' ingredients, often included in spray formulations, to produce synergistically toxic effects [56,57]. Inactive ingredients, alone, can have lethal and sublethal effects on honeybees [29,39]. Finally, we can only speculate why pesticide use in orchards had no effect on social bees in this study. In spite of their often larger size, social bees were found to be generally more susceptible to pesticides than solitary bees [65]. While a small sample size of social bees may have made measuring an effect of spray regime difficult, solitary and social bees differ in their life histories, including number of generations produced within a season, foraging distance, diet breadth, and when reproductives are produced; all of which may contribute to taxon-specific responses to toxins [28]. While we may not fully understand the mechanisms, this study is the first to document a direct, whole community response of wild bees to a full spectrum of conventional pesticide use, including fungicides, at the farm scale. Our findings support broadening protocols for bee toxicity testing of pesticides and expanding cautious use of pesticides to the entire growing season when wild bee pollinators are actively foraging in or near crops.

That natural areas not only provide nesting and foraging resources but also dampen the effect of pesticides on the wild crop pollinators extends the benefits natural habitats have for wild bees and their services. Given the high mobility of bees, the capacity of natural areas to buffer the negative effects of pesticides on wild bees could be attributed to (i) greater provision of resources and/or (ii) refuge from pesticides. Natural areas support crop pollinators by providing vital foraging and nesting resources for population establishment and growth that are not available in agricultural fields. Deciduous or mixed forests were the major natural landcover in our study. Before canopies have closed, these forests are important for early spring pollinators [53]. The more abundant and diverse the natural resources in a landscape, the larger, more diverse [54] and possibly more healthy [66] are the regional pool of bees available to forage within orchards.

Refugia from pesticide exposure, provided by natural, including semi-natural, area in the agricultural matrix, could foreseeably support healthy wild bee populations, as has been observed for natural enemies [67–69]. Conversely, bees foraging in landscapes dominated by agricultural areas where pesticides are applied, will have higher exposure risk even for pollinators surveyed in orchards with low PUI [62]. Interactions between pesticide regime and landscape have been observed previously by comparing bee diversity in organic versus conventional fields, with benefits of organic farming detected only in agriculturally intensified landscapes [70]. This pattern is attributed to higher floral resources typical in weedy organic fields within landscapes that offer few other floral resources. While this may

indeed be the case, the inability of intensified landscapes to buffer conventional pesticides could also contribute to such patterns. Though pesticides depress wild bee communities, apple's mass bloom may provide important foraging resources that could boost bee populations [71]. An interesting direction for future study would be to identify a threshold of pesticide use given different levels of surrounding habitat, under which orchards could have a net positive effect on bee populations owing to this mass bloom.

Evidence is building for the susceptibility of wild bee communities to pesticides in agricultural fields and landscapes [18,55,59,70,72]. Our findings suggest that heavy use of conventional pesticides, even some traditionally viewed as benign [39], can render our crops net sinks for bee populations. These effects are compounded by loss of natural habitat, which in itself can result in greater dependency of farms on pesticide inputs owing to loss of natural pest suppression [13], which ultimately reduces pollinator pools. Reliability of pollination by wild bees, therefore, relies on judicious use of pesticides and our ability to maintain, or create if necessary, a minimum threshold of natural area within agricultural matrixes. If landscape-level changes are not possible, local efforts such as plantings that boost local bee populations may help wild pollinators overcome the risks associated with pest management. Sound agri-management schemes aimed at sustaining wild bee pollination services will need to balance the benefits of pest management against the costs to wild pollinators, and do so with the understanding that such trade-offs will change depending on the landscape context. Practices that preserve, even enhance, wild bee

pollination services may also support additional ecosystem services, such as biological control.

Data accessibility. Data from this study have been made publically available at the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.t5n3t>).

Authors' contributions. All authors contributed to study design. M.G.P. co-coordinated the study, collected field and pesticide data, identified bees, led data management and analyses, and drafted the manuscript; E.J.B. co-coordinated study, collected field and pesticide data, identified bees and contributed to statistical analyses; J.G. collected field data and identified bees; J.E.L. conceived the use of PUI in this study and provided statistical advice; B.N.D. co-coordinated the study, collected field data and identified bees. All authors contributed significantly to revisions and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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