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A risk based pollination network for non-*Apis* bees demonstrates the importance of understory plant contamination

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Understanding the distribution of pesticides in the floral landscape is critical for land managers and regulators, particularly since identifying where exposure occurs is critical to pesticide mitigation. In this study, we developed a bee-plant network for a commercial sweet cherry (*Prunus avium* L.) system and the surrounding unmanaged floral habitat. We estimated the pesticide contamination of flowering plants in this network by trapping pollen from honey bee colonies, identifying the plant species of origin of the pollen, and relating this to the non-*Apis* bee visitation and toxicity of pesticide detections. Over 90 plant-bee interactions from non-*Apis* species were matched with honey bee collected pollen. By combining bee visitation and pollen data, we attributed the pesticide hazard to 33 plant genera. Unlike previous studies, we observed the greatest hazard to non-*Apis* bees did not come from visits to the crop or from pesticide drift off the orchard, but from contamination of an orchard understory plant (genus *Taraxacum*). The importance of this plant in pesticide exposure was related to both the hazard of the pollen and the frequency of visitation by non-*Apis* bees. Our findings caution against generalizing how non-*Apis* bee species become exposed to pesticides.

Keywords Pesticide hazard, Honey bee, Wild bees, Pesticide risk assessment

The yield of crops across the world are dependent on honey bee (*Apis mellifera)* visits[1]. Consequently, the well documented losses among honey bee colony stocks[2–5] has made the reduction of pesticide exposure a priority for regulators and land managers[6,7]. The increased awareness of the threat of pesticides to honey bees has also raised the profile of non-*Apis*, non-managed bees for protection from pesticide pollution. Non-*Apis* bees play an important role in the pollination of wild[8–10] and crop plants[11–15]. As the conservation of wild bees, in particular native bees, becomes more of a concern for regulators and researchers[16,17], there have been calls to broaden pesticide risk assessment to consider non-*Apis* species[18–22].

In the U.S., the Environmental Protection Agency (EPA) is responsible for estimating exposure of bees to a pesticide in its estimation of risk[23,24]. Variation in bee exposure under field conditions, however, is difficult to characterize owing to the patchiness of contamination across where bees nest, forage and collect nesting material[25,26]. Moreover, it is likely that patterns of exposure vary among bee taxa owing to differences in life history[27,28]. Life history traits that might influence exposure include differential contamination of nesting materials used by species[20,21,29] and how pesticide contaminated provisions may be diluted among nestmates in social taxa, such as honey bees, prior being fed to larva[25,30]. Additionally, while honey bees and non-*Apis* bees have similar numbers of P450 enzymes to detoxify pesticides[31], phylogenetic analysis has shown that some groups, including *Megachilidae,* lack CYP9Q-related genes which indicates that the detoxification of some insecticides may be lost in these groups[32].

An additional variable explaining how different bee taxa become exposed to pesticides may arise from preferences for different floral resources. While bee taxa visiting a bee-attractive crop may experience similar exposure after a pesticide treatment, it has been shown that preference for crop flowers varies among bee taxa[11,22,33–40]. Some of the preference is explicable by morphological compatibility between flower and bee species, particularly regarding flower corolla width and depth and bee size and tongue length[27,28]. Additionally, while some species such as honey bees exhibit a wide breadth of pollen collection (polylecty)[41–46], others exhibit pollen specialization and restrict their pollen foraging to plants within the same family (oligolecty) or within the same genus (narrow oligolecty)[8,47–49].

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The link between foraging preference by different bee taxa and their pesticide exposure remains unclear. While it has been demonstrated across multiple systems that pesticide exposure by bees represents a mosaic of pesticides that extend beyond the pesticide applications most proximate to the nest[43,50–56], in some cases the specific sources of contamination can been characterized. Pesticide contamination from one genus, *Spirea,* was identified as disproportionately contributing to the pesticide hazard within nursery plants[57]. In other studies, *Brassicaceae* and *Vitis vinifera* were identified as the primary contaminating pollen within daily collections of pollen samples[58]. Yet in other studies, the connection remains unclear. For example, recent work from blueberry showed that bumble bees appear to be more contaminated with pesticides applied to the crop than honey bees, but the source of the significant non-crop exposure could not be identified[55]. This echoes similar work in apple pollination which found high pesticide exposure to honey bees despite low apple pollen collection[43].

We looked to characterize the patterns of pesticide hazards experienced by different bee taxa in a major commercial crop (sweet cherry (*Prunus avium*)) surrounded by a plant community with high bee biodiversity (white oak savannah). We estimated pesticide hazards for different bee taxa by: (1) determining pesticide contamination of different flowering plant taxa using pollen collected by honey bees and (2) relating these to estimates of exposure using a bee-plant association network. By identifying the plant origins of the trapped pollen and weighting the pesticide levels in that pollen to the visitation of different bee genera across the plants in cherry orchards and the oak savannah, we were able to estimate the relative hazard associated with the foraging patterns of different bees. We used this method to compare: (1) the average pesticide hazard to each bee genera over a foraging year, (2) the aggregate hazard of each plant genera within a pollination network and (3) the per-visit hazard by bee genera. Finally, we used a pesticide hazard weighted network to infer patterns of hazard across the landscape.

Results

In this study, we collected pollen from honey bee colonies, identified the pollen sources through microscopy, tested pollen samples for pesticide residues, and matched these pesticide residue profiles with non-*Apis* bees collected from floral resources on the same site. This allows us to connect bee visitation in the landscape with pesticide residues from the specific plants on the same site. Therefore, this dataset consists of: bee specimens net-collected from production areas and oak habitat, pollen samples and the associated pesticide profiles, and floral resource assessments.

We collected 1592 bees over two years (2020, $n = 784$ and 2021, $n = 808$) in sweet cherry production areas ($n = 136$), fallowed cherry production cover cropped with mustard (*Brassica nigra*) ($n = 390$) and the surrounding oak savannah ($n = 1066$). We photographed 1060 plants representing 19 plant families and 33 plant genera associated with pollinator visitation; observations within the dataset were given research grade designation in 35% of observations ($n = 369$) and 94% ($n = 996$) of plants were identified to genus level.

We collected 136 species of non-*Apis* bees in 23 genera over the sampling period (supplementary material). In 2020, 52% ($n = 404$) non-*Apis* bees were collected after honey bee colonies had left cherry fields and therefore could not be associated with pesticide residues. Bees collected after pollen trapping ended in 2020 are incorporated into the species lists and plant-pollinator network, but are not included in the statistical analysis or visualizations of HQ-weighted analysis. During periods of monitoring overlap, where both bees and pollen were collected, plants foraged on by non-*Apis* bees were matched with the identified pollen tested for pesticides from honey bee colonies stationed nearby, 45% ($n = 538$) at the same site on the same date. Less than 10% of wild bees collected were from plants which were not collected in honey bee pollen traps ($n = 155$); of these interactions, the majority ($n = 85$) of bees were collected from plants in the genus *Lomatium*.

Pollen from each plant genera was associated with an average Hazard Quotient (HQ) value indicating the HQ value experienced per visit by any native bee (supplementary materials). Hazard Quotient is a commonly used estimation of pesticide hazard to individual colonies[59–61] and across landscapes[50,62–64]; it relates the pesticide residue in pollen to the toxicity of the pesticide[61,65,66]. For the primary genera of bees within the dataset, bee visits were associated with plants that had associated hazard quotient (HQ) values in over 67% of visits ($n = 965$). Bees from the genus *Andrena* visitation events (i.e. *Andrena* visiting a single floral resource) were associated with plants collected in honey bee colonies pollen traps (i.e. pollen that was tested for pesticides) in 77% of all visits. *Bombus* was associated 100% of visits. *Eucera* was associated 91% of visits. *Nomada* was associated with 83% of visits. *Osmia* was associated with pollen 94% of visits. Plant genera with high HQ values include: *Capsella*, *Lithophragma*, *Stellaria*, and *Taraxacum* which all were associated with average HQ values of ~ 1000 (supplementary materials). With the exception of *Stellaria* (bees collected, $n = 21$ and pollen collections $n = 2$), these were all exclusively understory plants within the cherry orchard or fallow orchard habitat. Pollen and bees were collected throughout the bee flight season (April to June).

The mean HQ values of the most frequently collected non-*Apis* bee genera (*Andrena*, *Bombus*, *Ceratina*, *Eucera*, *Halictus*, *Lasioglossum*, *Nomada*, and *Osmia*) were compared to the HQ values associated with honey bee colonies during the same year and bloom period (Fig. 1). These bee genera also had the largest overlap in visiting plant genera that were collected by honey bees in pollen, enabling assignment of pesticide exposure through plant visits. In 2021 during cherry bloom, *Bombus* and *Halictus* were excluded from analysis due to insufficient numbers of individuals. There were also insufficient numbers of *Bombus* to include after petal fall in 2021. There were significant differences in HQ values between focal bee genera in all sampling periods and both years. Analysis of cherry bloom in 2020 ($F(7, 390) = 6.761$, $p < 0.0001$) cherry bloom in 2021 ($F(6,115) = 3.719$, $p = 0.002$) and after petal fall in 2021 ($F(7,216) = 3.652$, $p = 0.001$) (Supplementary materials, Table S2) all indicated that bee genera ecperienced significantly different HQ values per floral visit. A post hoc Tukey test showed that the mean *Apis* HQ value was significantly different from *Andrena* ($p < 0.0001$), *Eucera* ($p < 0.0001$), *Nomada* ($p = 0.0001$), and *Osmia* ($p < 0.0001$) during cherry bloom in 2020 (Supplementary materials, Table S3). *Apis* bees experienced higher average HQ values when compared to non-*Apis* genera. During cherry bloom in

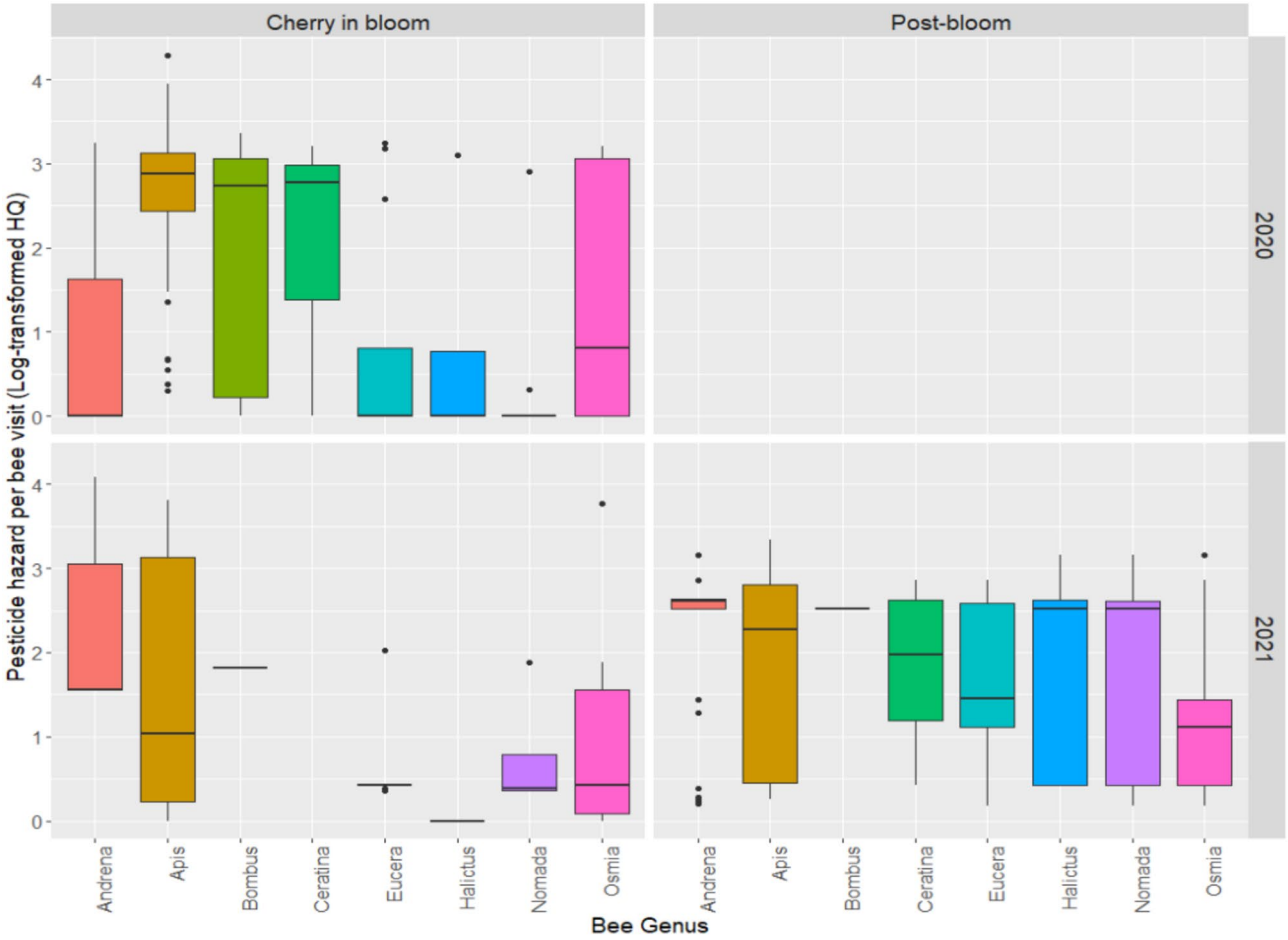

Fig. 1. A box and whisker plot showing the average HQ value per visit for focal bee genera, including honey bee in 2020 and 2021, stratified by when sweet cherry is in bloom and after petal fall. No post-bloom data was collected in 2020. The horizontal line indicates the median value (HQ); the boundaries of the box are the 25th and 75th percentiles. The whiskers represent the most extreme datapoints that are no more than 1.5 times the length of the box. Genera of bees with no plot indicate that insufficient numbers of the genera were collected during the time period to determine boundaries of the box and whisker plot.

2021, *Apis* was significantly different from *Andrena* ($p = 0.03$) but no other groups (Supplementary materials, Table S4). However, during 2021 cherry bloom *Andrena* had over three times the HQ value compared to *Apis*. Finally, after petal fall in 2021, *Apis* was significantly different from no other genera (Supplementary materials, Table S5).

To understand how plant-pollinator interactions changed in importance when HQ is considered, we created two networks for each year. The first is a basic network, which is constructed using standard plant-pollinator associations where the importance of the association between genera is demonstrated with the thickness of the bar connecting them (Figs. 2 and 3). During 2020, we collected 784 bees which represented 137 unique plant and pollinator interactions throughout the year. In 2021, we collected 807 bees which represented 95 unique plant and pollinator interactions throughout the year. *Osmia* was the most frequently detected bee genus in both years. In 2020, *Osmia* represented about 25% of the total interactions within the bee-plant interaction network (Fig. 2).

The second network we created is an HQ-weighted pollination network; in this network, the frequency of visitation and the HQ value of the plant both influence the thickness of the bar and relative importance of the interaction in the network. Each HQ weighted network simplifies the basic network interactions because any interactions where HQ = 0 are eliminated. Several plant genera change in the rankings of importance within the network when HQ weight is accounted for. The genus *Taraxacum* represents less than 15% of interactions within the basic network, yet increased to almost half of all interactions within the HQ weighted network. In contrast, the prominence of *Balsamorhiza* in the bee-plant association network was reduced when weighted by HQ is considered. In the basic network, *Balsamorhiza* represented just under 20% of all interactions, however in the hazard-based network it was reduced to 5% of interactions. Within the basic pollination network, *Osmia* is most frequently collected from *Balsamorhiza* and *Taraxacum* but it is clear that only *Taraxacum* represented a significant pesticide hazard to *Osmia* in 2020 (Fig. 2). As in 2020, *Taraxacum* visitation in 2021 represented more interactions in the HQ weighted network compared to the basic network, jumping from less than 5% of interactions to a quarter of all weighted interactions.

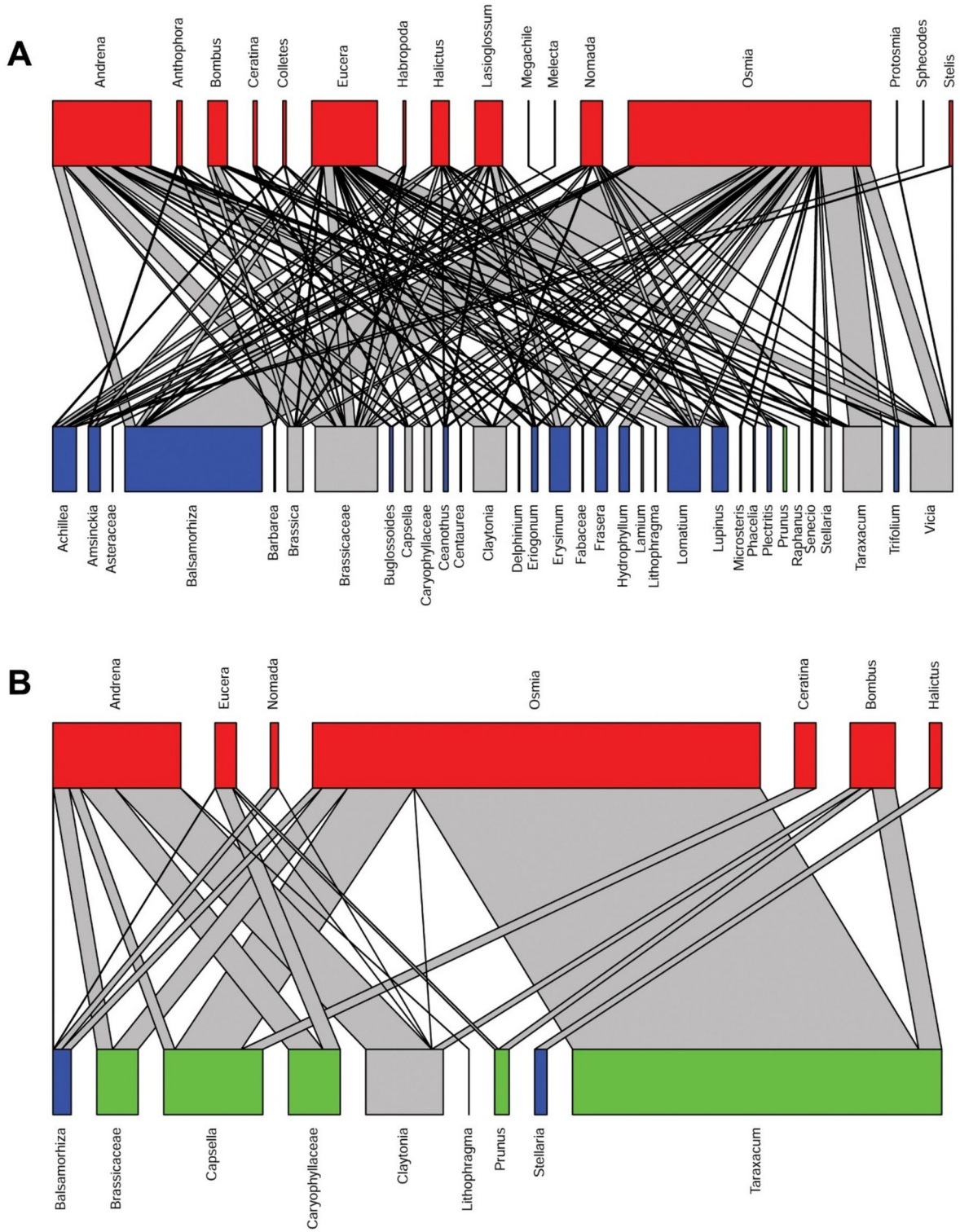

Fig. 2. A pollination network showing the relationship between wild bee visitation and plant genera in 2020. The thickness of the bars represents the number of visits from each bee genera to each plant genera. The basic network represents the interactions between plants and pollinator visits (**A**). The HQ network (Hazard Quotient Network) represents the network, considering the HQ values of each interaction, summed by plant and bee genera (**B**). Upper bars represent bee genera and lower bars represent plant genera in the pollination network. Plant genera found exclusively in oak savannah are shown in blue, those unique to cherry orchard and understory are in green, and plants shared between both areas are in gray.

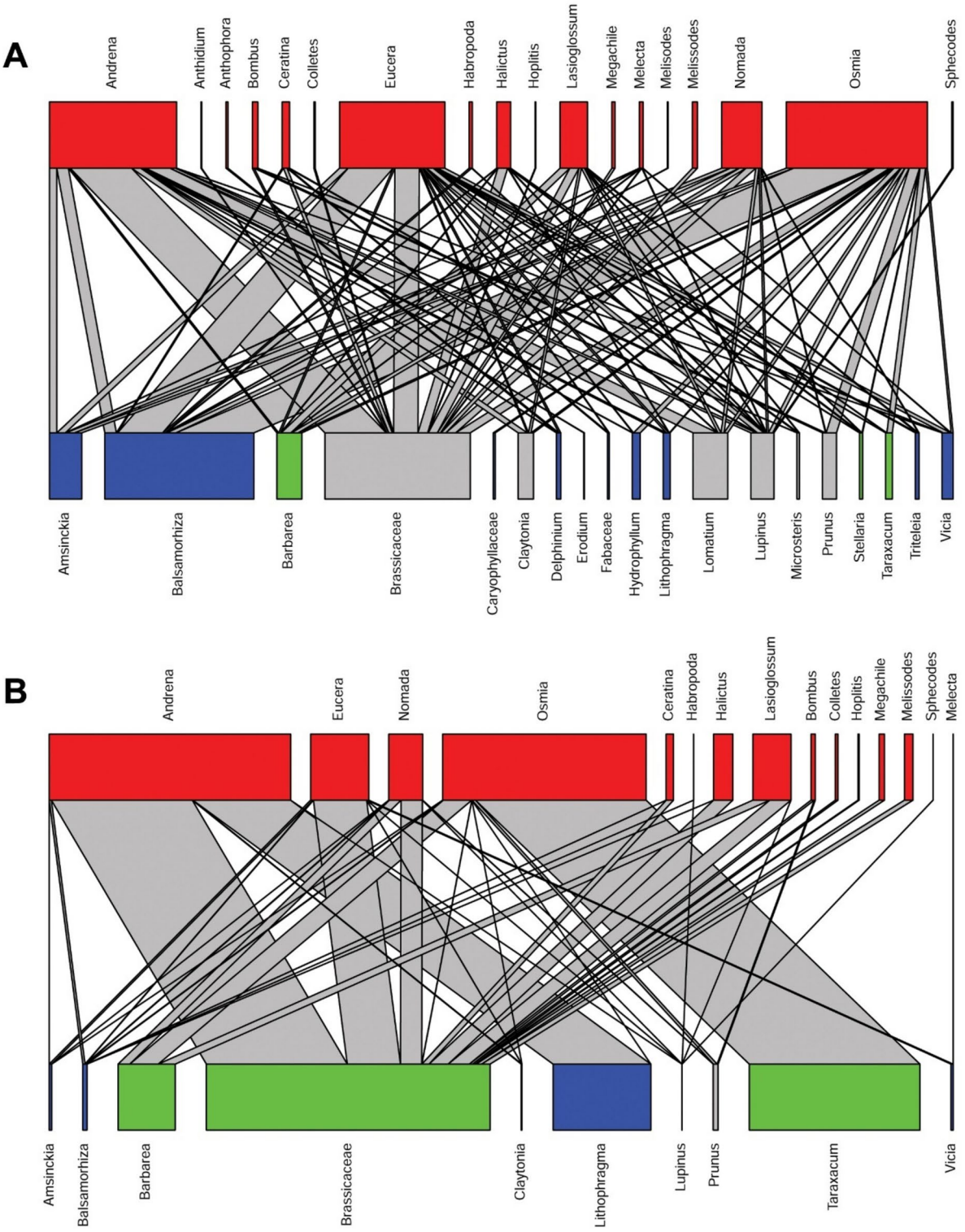

Fig. 3. A pollination network showing the relationship between wild bee visitation and plant genera in 2021. The thickness of the bars represents the number of visits from each bee genera to each plant genera. The basic network represents the interactions between plants and pollinator visits (**A**). The HQ network (Hazard Quotient Network) represents the network, considering the HQ values of each interaction, summed by plant and bee genera (**B**). Upper bars represent bee genera and lower bars represent plant genera in the pollination network. Plant genera found exclusively in oak savannah are shown in blue, those unique to cherry orchard and orchard understory are in green, and plants shared between both areas are in gray.

The importance of bee genera within the networks also changes when HQ values are considered. In 2021 and 2020, the highest number of interactions within the basic plant and pollinator network were represented by *Osmia*. In both 2020 and 2021, *Osmia* became more important within the HQ-weighted networks. For example, in 2020, the importance of *Osmia* within the network nearly doubled. *Andrena* species were a small proportion of interactions in both the weighted and basic networks in 2020. However, in 2021 *Andrena* were more frequently collected and associated with HQ values (Fig. 3). *Andrena* collected in mid-April of 2021 were exposed to the highest HQ values based on their foraging behaviors (Fig. 3).

In 2021, pollen sampling occurred throughout May when petal-fall had already passed in sweet cherry orchards. Cover crops in production areas (*Brassicaceae*) came into bloom during this period and represent a large source of both forage and pesticide hazard within the network. *Andrena*, *Eucera*, and *Nomada* were frequent visitors to plants in the Family *Brassicaceae* and this represents the majority of each bee genera's pesticide hazard. The most common species collected from *Brassicaceae* were *Andrena pallidifovea* ($n = 19$), *Andrena aculeata* ($n = 15$), and *Nomada edwardsii* ($n = 15$). These three species represent only 28% of the total visitors to *Brassicaceae*, which was visited by 52 individual species. On asters, *Osmia* dominated the collections. *Balsamoriza* and *Taraxacum* bloom during the same periods and attracted *Osmia* visitors. *Balsamoriza* was dominated by *Osmia californica* ($n = 153$), *Osmia montana* ($n = 27$), and *Osmia nigrofrons* ($n = 14$). These three species represent 69% of visitation to *Balsamoriza*. Similarly, *Taraxacum* was predominately visited by *Osmia*; specifically *O. atrocyanea* ($n = 2$), *O. californica* ($n = 39$), *O. kincaidii* ($n = 2$), and *O. montana* ($n = 1$). Together, *Osmia* represents 90% of visitors to *Taraxacum*.

Discussion

We provide evidence of the differential exposure of bee taxa based their patterns of visitation to plant genera in and around an agricultural system. In doing so, we demonstrate that in the sweet cherry system in Oregon bee taxa face dissimilar hazards. We identify the major source of exposure to non-*Apis* bees is restricted to one genus (*Osmia*) visiting plants found primarily on the orchard floor (*Taraxacum*). These findings not only provide cherry growers with very specific guidance for mitigating pesticide hazards to bees, but more significantly, emphasize the importance of gathering bee-plant association data for understanding these hazards in other agricultural systems.

Examining pesticide contamination over time, we found evidence that bee genera were exposed to different HQ values in both years and all bloom periods (Fig. 1) (supplementary materials, table S2). Non-*Apis* bee pesticide hazard metrics were built from pollen samples which must compose at least 10% of the total honey bee pollen sample. During cherry bloom in 2020, *Apis* bees were exposed to the highest HQ values (1935 ± 679, supplementary materials S3) and all other bee genera experienced lower hazard with *Andrena*, *Eucera*, *Nomada*, and *Osmia* experiencing significantly lower HQ values. However, this same pattern was not consistent during cherry bloom in 2021 where *Andrena* experienced the highest pesticide hazard (3470 ± 2208, supplementary materials S4) and all other genera were not significantly different than *Apis*. After petal fall in 2021, *Andrena* was again exposed to the highest HQ value per-visit, however this was not statistically significant (supplementary materials, S5). In some ways, this indicates that *Apis* is an adequate stand-in for other bee genera, as in most cases within this study *Apis* would be a conservative exposure estimate. However, HQ values fail to capture where pesticide exposure occurs in a landscape and what mitigation measures can be taken to reduce it.

When considering pesticide hazard to non-*Apis* bee genera as visualized within plant-pollinator networks, the relative importance of plants changes within each year. This means that potential mitigation measures could change as well. Due to the shorter sampling period of 2020, the network is highly simplified when considering only plants with non-zero HQ values, reducing the number of plants in the network from 33 genera to only 9 genera. In both 2020 and 2021, *Taraxacum* pollen represented a more significant contribution of pesticide hazard to the network when compared to *Prunus* pollen. As *Taraxacum* was primarily present in understory habitat within orchards, this indicates that controlling blooming weeds in orchard aisles may be even more important to protecting non-*Apis* bees when compared to controlling pesticide contamination on cherry blossoms themselves. This comparison also indicates the importance of monitoring the same system over the foraging activity of bee genera. In 2020, *Brassicaceae* represented a low hazard pollen forage resource, yet when the monitoring scheme was expanded to include post-cherry-bloom monitoring periods, *Brassicaceae* became a significant source of pesticide contamination within the network. Some studies have analyzed pollen samples from the same sites over time[56,58], yet in most cases pollen is analyzed from a single site on a single date per year[43,57,67]. The ephemerality of pesticide detections within a system can mean that sampling systems at one time may miss differences in contamination across a landscape[25]. As in other studies, high HQ values can be detected in pollen for short episodes, followed by relatively low levels at the same site[57,58].

The results of this study can also be used to make recommendations on mitigation measures reducing pesticide exposure to bees. Controlling pesticide exposure on cherry bloom itself through: modifications to sprayers and chemistries (i.e. low drift adjuvants and less toxic chemistries)[68–70] and timing applications to maximize environmental degradation before bee visitation[71–73] (i.e. spraying at night) could reduce pesticide exposure to honey bees contracted to perform pollination services. However, while some studies suggest that additional forage available during pollination could reduce pesticide exposure[74–78], our study suggests that forage provided within a production area may increase pesticide hazard and disproportionately effect non-*Apis* bees. Mowing these areas to eliminate floral resources before pesticide applications could greatly reduce pesticide hazard to foraging non-*Apis* bees.

We focused on generic level differences in pesticide hazards among bees in our study, but believe that more insights may come from species-level analysis in the future. A case in point comes from drawing conclusions from our findings from *Osmia* generically to all *Osmia* species, particularly there interest in using *Osmia lignaria* (blue orchard mason bee) in cherry pollination as it has been demonstrated to improve pollination success in

combination with honey bees[13,15]. Growers in our study, however, did not use managed *O. lignaria* and wild populations were difficult to detect; with only only one specimen collected from *Balsamorhiza* throughout the study. As *O. lignaria* may have a broader diet breadth than many of the Asteraceae focused *Osmia* species, it is unclear from our study whether the patterns we observed for Osmia generically would apply to O. *lignaria*.

The pesticide hazard represented by specific chemistries also changed over time. In 2020 during cherry bloom, Pyriproxyfen was detected 46 times but only 6 times during bloom in 2021 (supplementary materials, S6). Pyriproxyfen is a juvenile hormone analogue which is used in sweet cherry production to treat leafrollers but is only applied during dormancy[79]. Given that Pyriproxyfen requires 300 days minimum before cherry harvest, it is likely that this residue was not coming from sweet cherry orchards but rather drifting from another source. One potential source are nearby pear orchards (*Pyrus spp.*), where producers use Pyriproxyfen to control pear psylla (*Cacopsylla pyricola*)[80,81]. Imidacloprid was detected during cherry bloom in 2020 and after petal fall in 2021; due to the acute toxicity of imidacloprid to bees, it was a large contributor to pesticide risk in *Brassicaceae* samples where it was detected. Imidacloprid can be applied to cherry after bloom to control multiple pests with spotted wing drosophila (*Drosophila suzukii*) representing a major pest growers seek to control in the region.

While honey bees and non-*Apis* bees are documented to forage on similar resources in many other studies[82–86], this study highlights a surprisingly tight association between non-*Apis* bees and the remnant white oak savannah surrounding cherry orchards. The distinctiveness of the system may be explicable by the lack of wild *Prunus* species in historic oak savannah plant communities. Consequently, while *Osmia* have been associated with increased fruit set and pollination success[15,87–90] in other systems, the most prominent species we observed were primarily Asteraceae specialists (e.g., *Osmia montana*). Alternatively, the strong preference of honey bees for cherry in our system may have resulted in the competitive exclusion of non-*Apis* bees from visiting cherry[91,92].

Paradoxically, it is the strong preference for the native spring Asteraceae such as the genus *Balsamorhiza* that may explain the patterns of pesticide exposure for *Osmia*. While *Balsamorhiza* was largely free of toxic pesticide residues, their preference Asteraceae resulted in them foraging on the orchard floor on *Taraxacum* at rates higher than other bee genera. Such subtle patterns would be overlooked by current approaches of modeling exposure conducted by EPA in its risk assessment for bees, which assume a static association between bee and plant taxa[23,93]. By measuring the relative pesticide contamination within a bee-plant association network we are able to go beyond the studies that are only able to emphasize the importance of non-focal crop pollen as a significant source of pesticide contamination[50–53]. Furthermore, EPA pesticide risk assessments rely on honey bee toxicity and foraging behaviors to estimate environmental hazard to all bees[23,94]. This work adds to the significant body of literature which indicates non-*Apis* bees may be exposed in different pathways; not just through differences in life history[20,21,26,29,95], but also through differences in foraging patterns[33,56,96].

While the significance of *Taraxacum* contamination was observed across both years of our study, we noted that *Capsella* was only significant in 2020 and *Brassicaceae* in 2021. Our study also demonstrates that although the interactions occurring within the landscape are diverse and primarily occur in the white oak savannah, the interactions with high pesticide hazard occur in the production areas for non-*Apis* bees. In 2020, four of five primary contributors to pesticide hazard within the network were associated with cherry production and understory (*Brassicaceae*, *Capsella*, *Caryphyllaceae*, and *Taraxacum).* A similar pattern was observed in 2021, where three of the four primary contributors to the hazard network were associated with cherry production (*Barbarea*, *Brassicaceae*, *Lithophragma*, and *Taraxacum).* If non-*Apis* bees had been excluded from production areas, pesticide hazard associated with visits would have reduced to less than a quarter of the pesticide hazard in both years. That is, through both the frequency of visitation and strength of pesticide hazard, production areas and understory plants become the primary source of pesticide contamination for non-*Apis* bees in these areas. Importantly, over half of all the visitors to *Brassicaceae*, *Taraxacum*, and *Balsamorhiza* were *Osmia*, with *O. californica* being the most abundant.

Many efforts have been made to understand honey bee pesticide exposure within a landscape[57–60] and similar work has been done to estimate non-*Apis* bee pesticide exposure[22,55,97–99]. A bee's pesticide exposure in a field is the combination of the patchiness of contaminated floral resources and the foraging behavior of the bee[25]; our study combines the foraging behavior of non-*Apis* bees in the field with differential contamination of pollen to understand pesticide exposure and hazard in a novel way. Nearly half of non-*Apis* bees collected during pollen trapping periods were matched with site and date specific pesticide detections collected from honey bees. Yet, pollen samples collected from honey bee colonies were comprised of predominantly cherry pollen (*Prunus*)[100]. In previous work, non-focal crop pollen and crop pollen were similarly contaminated within the landscape; meaning that non-focal crop pollen did not represent a refuge from pesticide contamination for non-*Apis* bee species[43,52,55,101,102]. This highlights the significant overlap in honey bee and non-*Apis* bee foraging behavior[39,84,85,103,104] and the variation in pesticide contamination which reaches honey bee colonies[25,100,105]. Moreover, our study also demonstrates that pesticide contamination after petal-fall in the pollinated crop increased pesticide hazard to non-*Apis* bees. This suggests that bees may be exposed to higher HQ pollen resources over the course of a season after petal fall[106,107] (as in 2021) or it may reflect the high variation in detected HQ values at a colony as a result of the patchiness of contamination[57,58].

This study does not address the toxicity of pesticides to non-*Apis* bees, which may distort some aspects of the findings. Because toxicological data is widely available only for honey bees[108–111], it is therefore it is common to use honey bee toxicity data as a surrogate for all bees[29,55,112,113]; similarly, our study relies on this data to represent toxicity to all bees. Some comparisons between honey bee toxicological data and non-*Apis* bee toxicological data indicate that honey bees are more sensitive to pesticides[114,115]. However, other literature indicates the opposite: that non-*Apis* bees may be more sensitive to pesticide exposure, especially regarding sublethal impacts of pesticide exposure[116–118]. This disconnect could lead to a mis-estimation of pesticide hazard to non-*Apis* bees. Additionally, HQ has been criticized in the literature for its simple, aggregate hazard approach[57,58,63,65,66], even by these authors. It is well documented that honey bees are exposed to a mixture of pesticides throughout

their foraging season in pollen and bee bread[56,58–60,119–121], and that these mixtures lead to synergies in pesticide toxicity, increasing hazard[122–124]. However, HQ captures none of these subtleties[65,66] and how changes in HQ over time relate to changes in bee health and overall risk is not well understood[59,65,66]. Instead of using HQ as a definitive stand-in for pesticide hazard, the goal of this work is to understand how weighting interactions by the HQ value of each visit change the importance of the plants in the network.

Pesticide residues found in nectar, on leaf surfaces, sediment, plant resins or water are also not accounted for in our pesticide hazard estimates, although bees may contact or ingest pesticide residues through these routes exposing adults and larvae[20,21,125]. Importantly, pollen typically has higher pesticide residues when compared to nectar collected from the same plants[126]. Perhaps most significantly for non-*Apis* species, visitation by males and kleptoparasitic species can comprise a large number of visits, yet both groups do not collect pollen[127]. Therefore, pesticide exposure may be distorted as an overestimation of pesticide exposure for these groups as nectar represents their primary floral foraging resource.

In conclusion, the pesticide contamination hazard to managed honey bees and non-*Apis* bees are similar through the lens of HQ. However, the source of this pesticide exposure is different and requires different mitigation strategies to address these concerns. Non-*Apis* bees are experiencing pesticide risk through drift onto understory plants and mass blooming cover crop plantings later in the pollination season, when most honey bee colonies have been moved to the next crop in their circuit. Honey bees are exposed through a diversity of pathways, but their strong presence in the orchard bloom indicates addressing applications to cherry bloom would benefit commercial colonies. This challenges the assumption that bees of different genera are exposed in the same way and indicates that different mitigation measures may be needed for the protection of each group.

The state of Oregon is particularly well positioned to resolve pesticide hazard to wild bees because it has one of the largest contemporary bee-plant interaction networks, spanning over 200,000 connections[128–130]. This research demonstrates that pesticide hazard to non-*Apis* bees can be approximated by honey bee collected pollen and yet al.so challenges that the mechanisms of exposure are the same. Future research could continue to investigate competition between honey bees and wild, non-*Apis* bees within these landscapes and illuminate how unequal pesticide contamination across a landscape can impact bee genera.

Methods

Location

This study was conducted over two years on sweet cherry production (*Prunus avium* L., ($n = 12$ sites in 2020, $n = 14$ sites in 2021) in the Columbia region. The Colombia plateau is characterized by arid sage-brush steppe and grasslands but was historically dominated by white oak savanna (*Quercus garryana)* with over 800 species of wildflower present[57,58]. The area is now farmed with tree fruit, including sweet cherry, pear, and apple production. Sites were located at least 2 km apart when possible, resulting in some potential overlap in the foraging radius of honey bee hives from different sites. Sites were located an average of 2.01 ± 0.8 km apart (Fig. 4). None of the growers used organic farming techniques, but instead relied on standard agrochemicals and agronomic practices. Consent was obtained from the land manager in the form of a letter of support for the project; although the land was owned by different individuals, it was managed by the same organization.

Land cover type surrounding each site was determined using the National Land Cover Database from the US Geological Survey (https://www.usgs.gov/centers/eros/science/national-land-cover-database*)* in 2021. Land use was determined as cherry production, natural land cover (oak savannah fragments), other agricultural use (all crops excluding cherry) and other (urban or other usage) (Fig. 4) at a 30 m-scale.

In addition to cherry orchards, sites included considerable areas of remnant white oak savannah (shrubland, Fig. 4), including narrow strips of land that were too steep to farm that created a network of natural area in and through the orchards. The area included grass agricultural headlands and orchard rows that frequently included blooming forbs, other agricultural areas, particularly other tree fruits and *Brassica napus* subsp. *napus* cover crop, which was used by cherry growers prior to replanting cherry orchards. White oak savannah is an insect-rich habitat[59] where an estimated 1–5% of the habitat remains intact[60] and therefore the juxtaposition of agricultural land with this habitat could provide potential for wild bee species to be exposed to pesticides.

Pollen collection, identification, and testing

Pollen trapping was conducted as in Topitzhofer et al. (2021). When pollen traps were attached, bees were allowed to acclimate and then traps were engaged for 24–48 h during good foraging weather (i.e. periods of time without rain or temperatures below 12.8 °C). Pollen was collected in coolers and stored in a − 20 °C freezer until analysis. In 2020, commercial beekeepers were contacted and volunteered to participate in this study. Strongly foraging hives (> 50 returning foragers per minute when temperatures were above 20 °C) from twelve sites were selected in 2020 with two trapping events per site, both occurring during cherry bloom. Commercial pollination in sweet cherry is usually no more than two and a half weeks. Therefore, in 2021, this was expanded to include both twelve commercial hives and fourteen hives from Oregon State University on the same sites to extend the pollen trapping season. With these additional colonies on site, we were able to trap for five pollen collection periods over two months. These samples were divided into those which were taken during cherry bloom and after cherry bloom. Therefore, there are three pools of pollen samples: 2020 during cherry bloom, 2021 during cherry bloom, and 2021 after petal fall in cherry.

The pollen samples collected from the field were separated into color groups using the Pantone Color Guide from a 10 g subsample of the whole[56,61]. Each color group was then acetolyzed with a modified protocol for 0.25 g samples[61,62] which removes the lipid coat and allows identification of the pollen protein exine[63,64]. Pollen grains were then identified with light microscopy using DiscoverLife keys (http://www.discoverlife.org) and then confirmed with PalDat Palynological Database (https://www.paldat.org) and Cornell Pollen Grains Reference

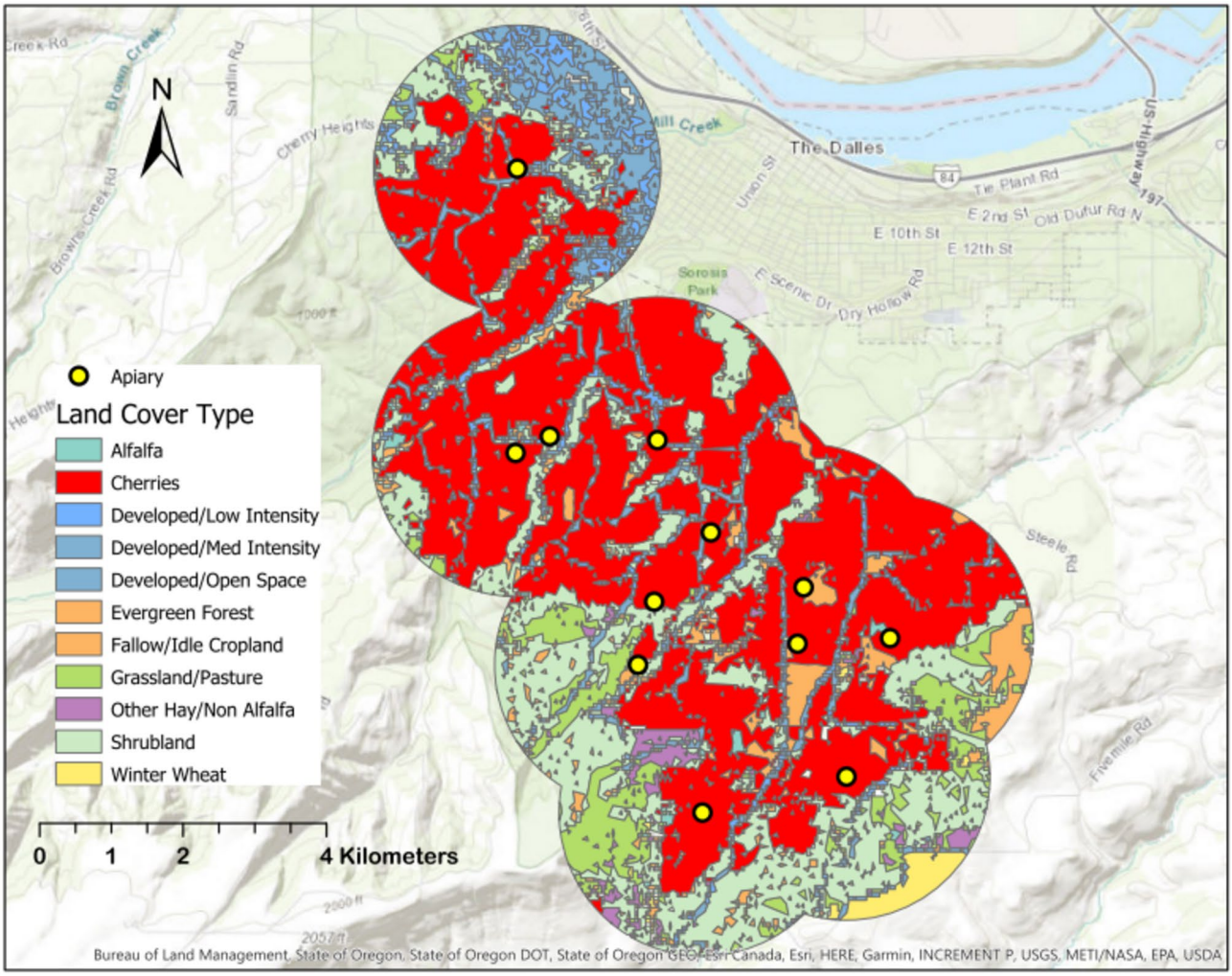

Fig. 4. A map showing the location of sites where pollen was trapped from commercial honey bee colonies engaged in pollination contracts for cherry southwest of the town of The Dalles, Oregon. A buffer of 3 km radius appears around each apiary site showing different surrounding land cover types from Cropscape (2020).

Library (https://blogs.cornell.edu/pollengrains). Identification was performed to plant genus and identified as pollen from each of the floral resources in bloom during the collection period.

Each pollen sample collected was processed for pesticide residue analysis as in Carlson et al. (2024); in brief, pollen samples were analyzed as composite samples (representative samples from the whole) and segregated into color groups. Both groups (composite and color-sorted subsamples) were tested for pesticide residues at Synergistic Pesticide Laboratory in Portland, OR. QuEChERS protocol[66,67] with both LC/MS-MS and GC/MS methods for pollen analysis[68]. In this way, each pollen sample had a unique pesticide profile associated with each plant genera found within the total sample and a composite sample pesticide residue profile. Composite samples were used as an estimate of *Apis* exposure. Sorted component samples were identified and matched with non-*Apis* bee visitation to identify sources of pesticide contamination within the landscape.

Next, Hazard Quotient (HQ) was calculated for all samples[65,69,70]. HQ is a unitless value which relates the residue detections of a pesticide in bee matrices to the toxicity of that pesticide to individual honey bees, and is used to understand aggregate pesticide hazard entering the colony[70,71]. HQ was calculated for each sample by taking the pesticide residues detected (ppb) and then dividing this value by the LD_{50} of the pesticide. The LD_{50} values used for each pesticide were taken from either Traynor et al. (2016) supplementary table or the EPA EcoTOX database (https://cfpub.epa.gov/ecotox/) using the oral LD_{50} for the pesticide to approximate dietary pesticide toxicity (see Carlson et al. 2024 for a complete pesticide residue analysis).

Bee collection

Bee sampling was conducted in alignment with the Oregon Bee Atlas (OBA) methodology[72]. Sites were broken into two habitat types: cherry production, including cherry orchard and understory, and oak savannah fragment, including all floral resources within 500 m of the cherry habitat.

Bees were collected using a variable length transect aerial netting for either 15 sampling minutes (cherry production) or 30 sampling minutes (oak savannah)[73]. Habitats required different sampling durations due to the

complexity of the habitats and the ability to access floral resources. Differences in sampling effort were controlled by analyzing pesticide contamination in a per-visit metric. Bees sampled at the same site and date, from the same floral resource were pooled together in the same sample identifier. All collections contained the same information: (a) Sample ID number, (b) date and time of sample collection, (c) latitude and longitude of the collection, (d) photo and sample description of the floral resource, d) number of bees collected. This was collected on the mobile phone app iNaturalist (/www.inaturalist.org/) associated with the community project Oregon Bee Plants in and Around Cherry Orchards (https://www.inaturalist.org/projects/oregon-bee-plants-in-and-around-cherry-orchards). This associates each bee observation with an image of the floral resource including images of the flowers, leaves, and whole plant. The floral resource was then identified through iNaturalist volunteer base. This data was then exported into a spreadsheet for verification and processing. Specimen determinations of non-*Apis* bees were made by Lincoln Best, the taxonomist with the Oregon Bee Atlas[72,74–77]. Bees were identified to genus level and then to species and exemplar specimens vouchered at the Oregon State Arthropod Collection. A list of bee species can be found in supplementary materials (Table S3).

There were two possible outcomes for associating a wild, non-*Apis* bee in the bee collection with the HQ of a pollen sample. First, if a bee was collected from a sample that honey bees also collected pollen from (on the same site and the same day), then the association considered a direct association. These direct associations are used in statistical testing and visualizations for HQ-weighted analysis. Second, if a bee was collected upon a floral resource which no honey bee collected pollen was associated with that plant, then the bee is noted in the collection, but not included in any analysis; these bees are included in traditional plant-pollinator network visualizations.

Floral assessment

During the bee sampling periods, floral resources were assessed for each habitat. Cherry orchard, understory, and oak required different sampling strategies to assess bloom state and the floral resources present in each habitat type. Cherry understory was assessed using a 0.5 by 0.5 m quadrat sampling method[59,78,79] (Supplementary materials, Figures S1–S4). In summary, quadrats were thrown along the understory and photographed. Photographs were then identified using visual assessments of coverage for each plant species[78–80]. Floral resources in oak fragments were assessed using the nearest neighbor technique[80–82] and images of each neighbor were photo-vouchered in iNaturalist (Oregon Bee Plants in and Around Cherry Orchards) along with bee collection data (Supplementary materials, Table S3 and S4).

Statistical assessment

All statistical calculations and visualizations were performed in the R statistical environment[83]. Bee sampling periods, floral resource data, and pollen identified to plant genera were aligned so that each bee was associated with the pollen identified from the plant that the bees were collected on.

Next, pollination networks were constructed in R (bipartite) by year for both standard pollination network analysis[12,84,85] and weighted HQ network analysis. For the construction of the weighted HQ network, plant genera which were not detected in honey bee collected pollen or which had HQ values of 0 (no pesticide contamination detected) were dropped from the network. The number of bee visits to a plant genera were multiplied by the median HQ value for that plant genera, providing a weighted estimate of the HQ contribution of the plant to the pollination network by bee genera detected.

To determine a single estimated value of HQ for each bee genera present, estimated HQ values were calculated for each bee genera over the entire year by combining the percentage of visits to each floral resource and the HQ values of each floral resource. This creates a weighted pesticide hazard (HQ) value that represents the average HQ value for a non-*Apis* bee visiting a floral resource which can be compared to the HQ values of composite pollen samples collected from honey bee colonies. For example:

$$\mathrm{HQ}_{\text{bee genera A}} = \left(\mathrm{HQ}_{\text{plant 1}} * \text{percentage of visits}_{\text{plant 1}}\right) + \left(\mathrm{HQ}_{\text{plant 2}} * \text{percentage of visits}_{\text{plant 2}}\right) + \ldots \left(\mathrm{HQ}_{\text{plant n}} * \text{percentage of visits}_{\text{plant n}}\right)$$

We used one-way ANOVA to test the null hypothesis that HQ values among bee genera were the same. Next, when we found sufficient evidence to reject the null hypothesis, we separated bee genera HQ values using Tukey-Kramer honest significant difference (HSD) tests. Pollen samples were pooled into during and after cherry bloom for these tests. The assumptions of normal error distribution and homoscedasticity for ANOVA and t-tests were confirmed by an examination of residuals for composite and color sorted subsamples at peak bloom.

Data availability

The datasets analyzed during the current study are available from the corresponding author on reasonable request. Additional information is included in the published article and its supplementary information files.

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References

1. Klein, A. M. et al. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* **274**, 303–313 (2007).
2. Bruckner, S. *et al. 2018–2019 Honey Bee Colony Losses in the United States: Preliminary Results*. https://beeinformed.org/wp-content/uploads/2019/11/2018_2019-Abstract.pdf (2019).

3. McMenamin, A. J. & Genersch, E. Honey bee colony losses and associated viruses. *Curr. Opin. Insect Sci.* **8**, 121–129. https://doi.org/10.1016/j.cois.2015.01.015 (2015).
4. van Engelsdorp, D. et al. 'Entombed Pollen': A new condition in honey bee colonies associated with increased risk of colony mortality. *J. Invertebr. Pathol.* **101**, 147–149 (2009).
5. Ellis, J. D., Evans, J. D. & Pettis, J. Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. *J. Apic. Res.* **49**, 134–136 (2010).
6. Obama, B. Presidential memorandum: Creating a federal strategy to promote the health of honey bees and other pollinators. *Improv. Heal. Honey Bees Other Pollinators Natl. Strateg. Res. Action Plan* 221–225 (2014).
7. The Office of the Inspector General & United States Environmental Protection Agency. EPA Needs to Determine Strategies and Level of Support for Overseeing State Managed Pollinator Protection Plans OFFICE OF INSPECTOR GENERAL Ensuring the safety of chemicals. (2019).
8. Roof, S. M., DeBano, S., Rowland, M. M. & Burrows, S. Associations between blooming plants and their bee visitors in a Riparian Ecosystem in Eastern Oregon. *Northwest Sci.* **92**, 119–135 (2018).
9. Galpern, P., Johnson, S. A., Retzlaff, J. L., Chang, D. & Swann, J. Reduced abundance and earlier collection of bumble bee workers under intensive cultivation of a mass-flowering prairie crop. *Ecol. Evol.* **7**, 2414–2422 (2017).
10. Carman, K. & Jenkins, D. G. Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats. *Biol. Conserv.* **202**, 110–118 (2016).
11. Winfree, R., Gross, B. J. & Kremen, C. Valuing pollination services to agriculture. *Ecol. Econ.* **71**, 80–88 (2011).
12. Nooten, S. S., Odanaka, K. & Rehan, S. M. Characterization of wild bee communities in apple and blueberry orchards. *Agric. For. Entomol.* **22**, 157–168 (2020).
13. Ward, R., Whyte, A. & James, R. R. A tale of two bees: Looking at pollination fees for almonds and sweet cherries. *Am. Entomol.* **56**, 170–177 (2010).
14. Andrikopoulos, C. J. & Cane, J. H. Comparative pollination efficacies of five bee species on raspberry. *J. Econ. Entomol.* **111**, 2513–2519 (2018).
15. Bosch, J., Kemp, W. P. & Trostle, G. E. Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). *J. Econ. Entomol.* **99**, 408–413 (2009).
16. Sánchez-Bayo, F. & Wyckhuys, K. A. G. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
17 Hallmann, C. A. et al. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* **12**, e0185809 (2017).
18. Rundlöf, M. et al. Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature* **521**, 77–80 (2015).
19 Thompson, H. M. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). *Apidologie* **32**, 305–321 (2001).
20 Kopit, A. M. & Pitts-Singer, T. L. Routes of pesticide exposure in solitary, cavity-nesting bees. *Environ. Entomol.* **47**, 499–510. https://doi.org/10.1093/ee/nvy034 (2018).
21 Stoner, K. A. Current pesticide risk assessment protocols do not adequately address differences between honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.). *Front. Environ. Sci.* **4**, 1–8 (2016).
22. Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E. & Danforth, B. N. Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proc. R. Soc. B Biol. Sci.* **282**, 20150299 (2015).
23. US EPA, EAD & CDPR. White Paper in Support of the Proposed Risk Assessment Process for Bees. 1–275 (2012).
24. United States Environmental Protection Agency. *Guidance for Assessing Pesticide Risks to Bees* (2014).
25 Sponsler, D. B. et al. Pesticides and pollinators: A socioecological synthesis. *Sci. Total Environ.* **662**, 1012–1027. https://doi.org/10.1016/j.scitotenv.2019.01.016 (2019).
26. Raine, N. E. & Rundlöf, M. Pesticide exposure and effects on non-*Apis* bees. *Annu. Rev. Entomol.* **69**, 551–576 (2024).
27. Klumpers, S. G. T., Stang, M. & Klinkhamer, P. G. L. Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. *Ecol. Lett.* **22**, 469–479 (2019).
28. Harder, L. D. Morphology as a predictor of flower choice by bumble bees. *Ecology* **66**, 198–210 (1985).
29. Schmolke, A. et al. Assessment of the vulnerability to pesticide exposures across bee species. *Environ. Toxicol. Chem.* **40**, 2640–2651 (2021).
30. Sponsler, D. B. & Johnson, R. M. Mechanistic modeling of pesticide exposure: The missing keystone of honey bee toxicology. *Environ. Toxicol. Chem.* **36**, 871–881 (2017).
31. Jung, C., Noor-ul-Ane, M. & Mohamadzade Namin, S. Safety of Dwarf Honeybee, Apis florea, in relation with agricultural pest management. In *The future role of dwarf honey bees in natural and agricultural systems* (CRC Press, 2020).
32. Haas, J. Phylogenomic and functional characterization of an evolutionary conserved cytochrome P450-based insecticide detoxification mechanism in bees. *PNAS* **119**, 1–10 (2022).
33. Rollin, O. et al. Differences Of floral resource use between honey bees and wild bees in an intensive farming system. *Agric. Ecosyst. Environ.* **179**, 78–86 (2013).
34. Jha, S. & Kremen, C. Resource diversity and landscape-level homogeneity drive native bee foraging. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 555–558 (2013).
35. Gibbs, J., Elle, E., Bobiwash, K., Haapalainen, T. & Isaacs, R. Contrasting pollinators and pollination in native and non-native regions of highbush blueberry production. *PLoS ONE* **11**, 1–24 (2016).
36. Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2 (2002).
37. Nalepa, R. & Colla, S. R. Toward a wild pollinator strategy for Canada: Expert-recommended solutions and policy levers. *Facets* **8**, 1–18 (2023).
38. Martins, K. T., Albert, C. H., Lechowicz, M. J. & Gonzalez, A. Complementary crops and landscape features sustain wild bee communities. *Ecol. Appl.* **28**, 1093–1105 (2018).
39. Osterman, J., Theodorou, P., Radzevičiūtė, R., Schnitker, P. & Paxton, R. J. Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. *Agric. Ecosyst. Environ.* **315**, 107383 (2021).
40 Kline, O. et al. Biology, genetic diversity, and conservation of wild bees in tree fruit orchards. *Biology (Basel)* **12**, 31 (2023).
41. Topitzhofer, E. et al. Assessment of pollen diversity available to honey bees (Hymenoptera: Apidae) in major cropping systems during pollination in the Western United States. *J. Econ. Entomol.* **112**, 2040–2048 (2019).
42. Alaux, C. et al. A 'Landscape physiology' approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats. *Sci. Rep.* **7**, 1–10 (2017).
43. Mcart, S. H., Fersch, A. A., Milano, N. J., Truitt, L. L. & Böröczky, K. High pesticide risk to honey bees despite low focal crop pollen collection during pollination of a mass blooming crop. *Sci. Rep.* **7**, 1–10 (2017).
44. Richardson, R. T. et al. Honey bee pollen foraging ecology across an urbanization gradient. *bioRxiv* 824474 (2019) https://doi.org/10.1101/824474.
45. McMinn-Sauder, H., Richardson, R., Eaton, T., Smith, M. & Johnson, R. Flowers in conservation reserve program (Crp) pollinator plantings and the upper midwest agricultural landscape supporting honey bees. *Insects* **11**, 1–10 (2020).
46. Richardson, R. T. et al. Quantitative multi-locus metabarcoding and waggle dance interpretation reveal honey bee spring foraging patterns in Midwest agroecosystems. *Mol. Ecol.* **28**, 686–697 (2019).

47. Bosch, J., Martín González, A. M., Rodrigo, A. & Navarro, D. Plant-pollinator networks: Adding the pollinator's perspective. *Ecol. Lett.* **12**, 409–419 (2009).
48. Smith, C., Weinman, L., Gibbs, J. & Winfree, R. Specialist foragers in forest bee communities are small, social or emerge early. *J. Anim. Ecol.* **88**, 1158–1167 (2019).
49. MacIvor, J. S., Cabral, J. M. & Packer, L. Pollen specialization by solitary bees in an urban landscape. *Urban Ecosyst.* **17**, 139–147 (2014).
50. Tosi, S. et al. A 3-year survey of Italian honey bee-collected pollen reveals widespread contamination by agricultural pesticides. *Sci. Total Environ.* **615**, 208–218 (2018).
51. David, A. et al. Widespread contamination of wildflower and bee-collected pollen with complex mixtures of neonicotinoids and fungicides commonly applied to crops. *Environ. Int.* **88**, 169–178 (2016).
52 Long, E. Y. & Krupke, C. H. Non-cultivated plants present a season-long route of pesticide exposure for honey bees. *Nat. Commun.* **7**, 11629 (2016).
53 Krupke, C. H., Hunt, G. J., Eitzer, B. D., Andino, G. & Given, K. Multiple routes of pesticide exposure for honey bees living near agricultural fields. *PLoS ONE* **7**, e29268 (2012).
54. Knapp, J. L., Nicholson, C. C., Jonsson, O., de Miranda, J. R. & Rundlöf, M. Ecological traits interact with landscape context to determine bees' pesticide risk. *Nat. Ecol. Evol.* **7**, 547–556 (2023).
55. Graham, K. K. et al. Pesticide risk to managed bees during blueberry pollination is primarily driven by off-farm exposures. *Sci. Rep.* **12**, 1–16 (2022).
56. Graham, K. K. et al. Identities, concentrations, and sources of pesticide exposure in pollen collected by managed bees during blueberry pollination. *Sci. Rep.* **11**, 1–13 (2021).
57. Stoner, K. A., Cowles, R. S., Nurse, A. & Eitzer, B. D. Tracking pesticide residues to a plant genus using palynology in pollen trapped from honey bees (Hymenoptera: Apidae) at Ornamental Plant Nurseries. *Environ. Entomol.* **48**, 351–362 (2019).
58. Böhme, F., Bischoff, G., Zebitz, C. P. W., Rosenkranz, P. & Wallner, K. Pesticide residue survey of pollen loads collected by honeybees (*Apis mellifera*) in daily intervals at three agricultural sites in South Germany. *PLoS ONE* **13**, e0199995. https://doi.org/10.1371/journal.pone.0199995 (2018).
59. Traynor, K. S. et al. In-hive Pesticide Exposome: Assessing risks to migratory honey bees from in-hive pesticide contamination in the Eastern United States. *Sci. Rep.* **6**, 33207 (2016).
60. Traynor, K. S. et al. Pesticides in honey bee colonies: Establishing a baseline for real world exposure over seven years in the USA. *Environ. Pollut.* **279**, 116566 (2021).
61. Stoner, K. A. & Eitzer, B. D. Using a hazard quotient to evaluate pesticide residues detected in pollen trapped from honey bees (*Apis mellifera*) in Connecticut. *PLoS ONE* https://doi.org/10.1371/journal.pone.0077550 (2013).
62. Perry, E. D. & Moschini, G. C. Neonicotinoids in U.S. maize: Insecticide substitution effects and environmental risk. *J. Environ. Econ. Manage.* **102**, 102320 (2020).
63. Favaro, R. et al. Botanical origin of pesticide residues in pollen loads collected by honeybees during and after apple bloom. *Front. Physiol.* **10**, 1–18 (2019).
64. Friedle, C., Wallner, K., Rosenkranz, P., Martens, D. & Vetter, W. Pesticide residues in daily bee pollen samples (April–July) from an intensive agricultural region in Southern Germany. *Environ. Sci. Pollut. Res.* **28**, 22789–22803 (2021).
65. Carlson, E. A., Melathopoulos, A. & Sagili, R. The value of hazard quotients in honey bee (*Apis mellifera*) ecotoxicology: A review. *Front. Ecol. Evol.* **10**, 824992 (2022).
66. Thompson, H. M. The use of the Hazard Quotient approach to assess the potential risk to honeybees (Apis mellifera) posed by pesticide residues detected in bee-relevant matrices is not appropriate. *Pest Manag. Sci.* **77**, 3934–3941 (2021).
67. Frazier, M. T. et al. Assessing honey bee (Hymenoptera: Apidae) foraging populations and the potential impact of pesticides on Eight US Crops. *J. Econ. Entomol.* **108**, 2141–2152 (2015).
68. Reichenberger, S., Bach, M., Skitschak, A. & Frede, H. G. Mitigation strategies to reduce pesticide inputs into ground- and surface water and their effectiveness: A review. *Sci. Total Environ.* **384**, 1–35 (2007).
69. Felsot, A. S. et al. Agrochemical spray drift; assessment and mitigation—A review. *J. Environ. Sci. Health* **46**, 1–23 (2017).
70. Joshi, N. K., Leslie, T., Rajotte, E. G. & Biddinger, D. J. Chemosphere Environmental impacts of reduced-risk and conventional pesticide programs differ in commercial apple orchards, but similarly in fl uence pollinator community. *Chemosphere* **240**, 124926 (2020).
71. Otto, S., Lazzaro, L., Finizio, A. & Zanin, G. Estimating ecotoxicological effects of pesticide drift on nontarget arthropods in field hedgerows. *Environ. Toxicol. Chem.* **28**, 853–863 (2009).
72. Fornasiero, D. et al. Effect of spray drift reduction techniques on pests and predatory mites in orchards and vineyards. *Crop Prot.* **98**, 283–292 (2017).
73. Walker, E. K., Brock, G. N., Arvidson, R. S. & Johnson, R. M. Acute toxicity of fungicide–insecticide–adjuvant combinations applied to almonds during bloom on adult honey bees. *Environ. Toxicol. Chem.* **41**, 1042–1053 (2022).
74. Hrynko, I., Łozowicka, B. & Kaczyński, P. Comprehensive analysis of insecticides in melliferous weeds and agricultural crops using a modified QuEChERS/LC-MS/MS protocol and of their potential risk to honey bees (*Apis mellifera* L.). *Sci. Total Environ.* **657**, 16–27 (2019).
75. Smith, O. M., Gerdeman, B., Arrington, M., Spitler, H. & Devetter, L. W. Pollination, crop productivity, and arthropod and bird communities are marginally impacted by border vegetation in highbush blueberry production. *HortTechnology* **31**, 144–152 (2021).
76. Centrella, M. et al. Diet diversity and pesticide risk mediate the negative effects of land use change on solitary bee offspring production. *J. Appl. Ecol.* **57**, 1031–1042 (2020).
77. Rundlöf, M. et al. Flower plantings support wild bee reproduction and may also mitigate pesticide exposure effects. *J. Appl. Ecol.* **59**, 2117–2127 (2022).
78. Rundlöf, M., Lundin, O. & Bommarco, R. Annual flower strips support pollinators and potentially enhance red clover seed yield. *Int. J. Bus. Innov. Res.* **17**, 7974–7985 (2018).
79. Murray, K. & Jepson, P. C. *An integrated pest management strategic plan for sweet cherries in Oregon and Washington* (2018).
80. Blomquist, C. L. & Kirkpatrick, B. C. Frequency and seasonal distribution of pear psylla infected with the pear decline phytoplasma in California pear orchards. *Phytopathology* **92**, 1218–1226 (2002).
81. Nottingham, L., Orpet, R., Hilton, R. & DuPont, T. *Pear psylla integrated pest management*. (2022).
82. Gómez-Martínez, C., González-Estévez, M. A., Cursach, J. & Lázaro, A. Pollinator richness, pollination networks, and diet adjustment along local and landscape gradients of resource diversity. *Ecol. Appl.* **32**, 1–18 (2022).
83. Evans, E., Smart, M., Cariveau, D. & Spivak, M. Wild, native bees and managed honey bees benefit from similar agricultural land uses. *Agric. Ecosyst. Environ.* **268**, 162–170 (2018).
84. Roubik, D. W. & Wolda, H. Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. *Popul. Ecol.* **43**, 53–62 (2001).
85. Mallinger, R. E., Gaines-Day, H. R. & Gratton, C. Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PLoS ONE* **12**, e0189268 (2017).
86. Paini, D. R. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review. *Austral Ecol.* **29**, 399–407 (2004).

87. Tepedino, V. J., Alston, D. G., Bradley, B. A., Toler, T. R. & Griswold, T. L. Orchard pollination in Capitol Reef National Park, Utah, USA. Honey bees or native bees?. *Biodivers. Conserv.* **16**, 3083–3094 (2007).
88. Matsumoto, S., Abe, A. & Maejima, T. Foraging behavior of Osmia cornifrons in an apple orchard. *Sci. Hortic.* **121**, 73–79 (2009).
89. Ruber, B. G., Ckel, K. E., Veraars, J. E. & Ormann, C. F. D. On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* **42**, 564–576. https://doi.org/10.1007/s13592-011-0059-z (2011).
90. Matsumoto, S. & Maejima, T. Several new aspects of the foraging behavior of *Osmia cornifrons* in an apple orchard. *Psyche J. Entomol.* **201**, 1–6 (2010).
91. Weekers, T. et al. Dominance of honey bees is negatively associated with wild bee diversity in commercial apple orchards regardless of management practices. *Agric. Ecosyst. Environ.* **323**, 107697 (2022).
92. Goras, G. et al. Impact of honey bee (*Apis mellifera* L.) density on wild bee foraging behaviour. *J. Apic. Sci.* **60**, 49–61 (2016).
93. United States Department of Agriculture. *Attractiveness of Agricultural Crops to Pollinating Bees for the Collection of Nectar and/or Pollen*. (2015).
94. EPA. Technical Overview of Ecological Risk Assessment: Risk Characterization. 1–15 (2017).
95. Boyle, N. K. et al. Workshop on pesticide exposure assessment paradigm for non-*Apis* bees: Foundation and summaries. *Environ. Entomol.* **48**, 4–11 (2019).
96. Elliott, B. et al. Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic Appl. Ecol.* **50**, 169–180 (2021).
97. Hatfield, R. G., Strange, J. P., Koch, J. B., Jepsen, S. & Stapleton, I. Neonicotinoid pesticides cause mass fatalities of native bumble bees: A case study from Wilsonville, Oregon, United States. *Environ. Entomol.* **50**, 1095–1104 (2021).
98. Hladik, M. L., Vandever, M. & Smalling, K. L. Exposure of native bees foraging in an agricultural landscape to current-use pesticides. *Sci. Total Environ.* **542**, 469–477 (2016).
99. Kremen, C., Williams, N. M. & Thorp, R. W. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 16812–16816 (2002).
100. Carlson, E. A., Melathopoulos, A. P. & Sagili, R. R. The power to (detect) change : Can honey bee pollen be used to monitor for pesticide residue in the landscape ?. *PLoS ONE* **549024**, 1–24 (2024).
101. Zawislak, J., Lorenz, G., Adamczyk, J., Wiedenmann, R. & Joshi, N. K. Proportion of commodity crop pollens and pesticide contamination in honey bee diets in two different landscapes. *Environ. Adv.* **5**, 100116 (2021).
102. Hellwig, N., Schubert, L. F., Kirmer, A., Tischew, S. & Dieker, P. Effects of wildflower strips, landscape structure and agricultural practices on wild bee assemblages – A matter of data resolution and spatial scale?. *Agric. Ecosyst. Environ.* **326**, 107764 (2022).
103. Steffan-Dewenter, I. & Tscharntke, T. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* **122**, 288–296 (2000).
104. Worthy, S. H., Acorn, J. H. & Frost, C. M. Honey bees (*Apis mellifera*) modify plant-pollinator network structure, but do not alter wild species' interactions. *PLoS ONE* **18**, 1–22 (2023).
105. Simon-Delso, N., Martin, G. S., Bruneau, E., Delcourt, C. & Hautier, L. The challenges of predicting pesticide exposure of honey bees at landscape level. *Sci. Rep.* **7**, 1–10 (2017).
106. Danner, N., Molitor, A. M., Schiele, S., Härtel, S. & Steffan-Dewenter, I. Season and landscape composition affect pollen foraging distances and habitat use of Honey bees. *Ecol. Appl.* **26**, 1920–1929 (2016).
107. Garbuzov, M., Couvillon, M. J., Schürch, R. & Ratnieks, F. L. W. Honey bee dance decoding and pollen-load analysis show limited foraging on spring-flowering oilseed rape, a potential source of neonicotinoid contamination. *Agric. Ecosyst. Environ.* **203**, 62–68 (2015).
108. Botías, C. & Sánchez-Bayo, F. The role of pesticides in pollinator declines. *Ecosistemas* **27**, 34–41 (2018).
109. Sanchez-Bayo, F. & Goka, K. Pesticide residues and bees—A risk assessment. *PLoS ONE* **9**, e94482 (2014).
110. Laurino, D., Porporato, M., Patetta, A. & Manino, A. Toxicity of neonicotinoid insecticides to honey bees: Laboratory tests. *Bull. Insectology* **64**, 107–113 (2011).
111. Farruggia, F. T. et al. A retrospective analysis of honey bee (*Apis mellifera*) pesticide toxicity data. *PLoS ONE* **17**, e0265962 (2022).
112. Colla, S. R., Gadallah, F., Richardson, L., Wagner, D. & Gall, L. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodivers. Conserv.* **21**, 3585–3595 (2012).
113. Gradish, A. E. et al. Comparison of Pesticide Exposure in Honey Bees (Hymenoptera: Apidae) and Bumble Bees (Hymenoptera: Apidae): Implications for Risk Assessments. In *Environmental Entomology* vol. 48 12–21 (Entomological Society of America, 2019).
114. Arena, M. & Sgolastra, F. A meta-analysis comparing the sensitivity of bees to pesticides. *Ecotoxicology* **23**, 324–334 (2014).
115. Thompson, H. M. & Pamminger, T. Are honeybees suitable surrogates for use in pesticide risk assessment for non- Apis bees?. *Pest Manag. Sci.* **75**, 2549–2557. https://doi.org/10.1002/ps.5494 (2019).
116. Gill, R. J. & Raine, N. E. Chronic impairment of bumblebee natural foraging behaviour induced by sublethal pesticide exposure. *Funct. Ecol.* **28**, 1459–1471 (2014).
117. Stanley, D. A., Smith, K. E. & Raine, N. E. Bumblebee learning and memory is impaired by chronic exposure to a neonicotinoid pesticide. *Sci. Rep.* **5**, 16508 (2015).
118. Sandrock, C. et al. Sublethal neonicotinoid insecticide exposure reduces solitary bee reproductive success. *Agric. For. Entomol.* **16**, 119–128 (2014).
119. Tong, Z. et al. A survey of multiple pesticide residues in pollen and beebread collected in China. *Sci. Total Environ.* **640–641**, 1578–1586 (2018).
120. Traynor, K. S., vanEngelsdorp, D. & Lamas, Z. S. Social disruption: Sublethal pesticides in pollen lead to *Apis mellifera* queen events and brood loss. *Ecotoxicol. Environ. Saf.* **214**, 112105 (2021).
121. El Agrebi, N. et al. *Pesticide and veterinary drug residues in Belgian beeswax: Occurrence, toxicity, and risk to honey bees. Science of the Total Environment* vol. 745 141036 (Elsevier B.V., 2020).
122. Iverson, A., Hale, C., Richardson, L., Miller, O. & McArt, S. Synergistic effects of three sterol biosynthesis inhibiting fungicides on the toxicity of a pyrethroid and neonicotinoid insecticide to bumble bees. *Apidologie* **50**, 733–744 (2019).
123. Cedergreen, N. Quantifying synergy: A systematic review of mixture toxicity studies within environmental toxicology. *PLoS ONE* **9**, e96580 (2014).
124. Rand, E. E. D. et al. Detoxification mechanisms of honey bees (*Apis mellifera*) resulting in tolerance of dietary nicotine. *Sci. Rep.* **5**, 1–11 (2015).
125. Biddinger, D. J. & Rajotte, E. G. Integrated pest and pollinator management - adding a new dimension to an accepted paradigm. *Curr. Opin. Insect Sci.* **10**, 204–209 (2015).
126. Kyriakopoulou, K., Kandris, I., Pachiti, I. & Kasiotis, K. M. Collection and analysis of pesticide residue data for pollen and nectar Final Report. *Benki Phytopathol. Inst.* https://doi.org/10.2903/sp.efsa.2017.EN-1303 (2017).
127. Danforth, B., Robert, M. & Neff, J. *The Solitary Bees* (Princeton University Press, Princeton, 2019).
128. Best, L. et al. Oregon Bee Atlas: Wild bee findings from 2019. *Cat. Oregon State Arthropod Collect.* **6**, 1–13 (2022).
129. Best, L. et al. Oregon Bee Atlas: Native bee findings from 2018. *Cat. Oregon State Arthropod Collect.* **5**, 1–12 (2021).
130. Basman, A., Rampton, R. W., Melathopoulos, A. & Best, L. R. Melittoflora Version 1.0. https://agsci.oregonstate.edu/bee-atlas/melittoflora (2025).

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Author contributions
EAC conducted the experiments, performed the basic statistical testing and data analysis, performed the pollen identification using microscopy, and wrote the first draft of the manuscript. LB performed the bee identification. AM secured funding for the project, provided oversight on data analysis and edited the manuscript. SMN performed data analysis and edited the manuscript. RS secured funding for the project and oversight on the data analysis. All authors reviewed the manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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