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Diet diversity and pesticide risk mediate the negative effects of land use change on solitary bee offspring production

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Abstract:

1. Threats to bee pollinators such as land use change, high pesticide risk, and reduced floral diet diversity are usually assessed independently, even though they often co-occur to impact bees in agroecosystems.

2. We established populations of the non-native mason bee *O. cornifrons* at 17 NY apple orchards varying in proportion of surrounding agriculture and measured floral diet diversity and pesticide risk levels in the pollen provisions they produced. We used path analysis to test the direct and indirect effects of different habitats, diet diversity, and pesticide risk on emergent female offspring number and weight.

3. High proportions of agricultural habitat surrounding bee nests indirectly reduced the number of female offspring produced, by reducing floral diet diversity in pollen.

4. When the proportion of agriculture surrounding bee nests was high, bees collected increased proportions of Rosaceae in their pollen provisions, which marginally ($0.05<p<0.1$) increased fungicide risk levels in pollen. This, in turn, marginally reduced female offspring weight. In contrast, female offspring weight increased as proportions surrounding open habitat (wildflowers, grassland, pasture) increased, but this effect was not influenced by proportion Rosaceae or fungicide risk levels in pollen.

5. *Synthesis and applications.* Threats to bee health such as land use change, pesticide exposure, and changes in pollen diet composition are often studied in isolation. However, our results suggest that these threats can simultaneously influence one another to impact bee populations in the agroecosystems where we rely on them for pollination. By replacing surrounding agricultural habitats with more natural habitats, such as grasslands and pastures, we can increase floral diet diversity and reduce pesticide exposure in bee-collected pollen, resulting in healthier mason bee populations in apple orchards.

Keywords

Agroecosystems, bee decline, floral resources, *Osmia cornifrons,* pesticide toxicity, pollinator health, solitary bees, land use change

Introduction

Bees are essential crop pollinators, but there is rising concern that environmental threats to bee health could reduce pollination services in agroecosystems (Goulson, Nicholls, Botías, & Rotheray, 2015; Potts et al., 2010). A major threat to bee populations is land use change, specifically the conversion of natural habitats (forests, open meadows) to agricultural habitats. For instance, increasing agricultural habitats can negatively impact bees at the community level, reducing bee species richness and abundance (Connelly, Poveda, & Loeb, 2015; Mallinger, Gibbs, & Gratton, 2016), and at the population level, reducing reproduction, survival, and body size (Renauld, Hutchinson, Loeb, Poveda, & Connelly, 2016; Williams & Kremen, 2007). These impacts to bee populations will likely affect bee pollination services (see Jauker, Speckmann, & Wolters, 2016).Therefore, it is imperative that we understand the mechanisms through which land use change affects bees in agroecosystems.

Agricultural habitat can directly impact bees by reducing nesting resources (Threlfall et al., 2015) or floral resource availability, which can increase female foraging trip time (Westphal, Steffan-Dewenter, & Tscharntke, 2006), leaving nests vulnerable to predation and parasitism (Goodell, 2003). There is also evidence that increased agricultural habitat can affect bees indirectly, via a variety of mechanisms. Two of the more well-studied mechanisms include reduced floral diet diversity and increased pesticide risk.

For instance, decreasing grassland habitat can reduce floral species abundance and richness on farm edges (Power, Kelly, & Stout, 2012) and reductions in floral resource diversity have been shown to reduce bee species richness (Potts, Vulliamy, Dafni, Ne'eman, & Willmer, 2003), likely due to insufficient nutrition of less diverse diets (Donkersley et al., 2017; Lunau & Budde, 2007; Roulston & Cane, 1999). This suggests that the loss of natural habitats could negatively impact bees indirectly, by reducing floral resource diversity, and thus nutritional quality, in bee pollen diets.

Another mechanism through which land use change could impact bee populations is pesticide risk (or pesticide exposure in terms of toxicity to bees). Foraging bees can contact or ingest pesticide residues in air, water, soil, leaves, pollen, and nectar, and field-realistic doses have been shown to not only directly kill adult bees, but also reduce offspring production, foraging ability, and homing success (Alston et al., 2007; Gill, Ramos-Rodriguez, & Raine, 2012; Rundlöf et al., 2015). We can imagine that pesticide use, and therefore bee chemical exposure and risk, might be higher in agricultural environments.

Despite the above evidence that land use change might drive bee diet diversity and pesticide risk, few previous studies have investigated the impact of multiple, simultaneous threats to bee populations, and it is even rarer that studies explore the potential indirect and even interactive relationships that could exist between threats (but see Theodorou et al., 2016). Not only do we suspect that surrounding agricultural habitat might influence bees by reducing diet diversity and increasing pesticide risk, but there is also evidence that bee diet diversity could influence pesticides risk levels directly. Indeed, in agroecosystems, reduced floral diversity corresponds with increased pesticide exposure in honey bee collected pollen (Colwell, Williams, Evans, & Shutler, 2017), possibly because less diverse diets contain higher proportions of mass-flowering crop pollen, presumably with higher concentrations of pesticide residues. It is even possible that less diverse diets, with poor nutritional content, could hinder bee ability to detoxify agrochemicals, such that the two variables together would have an exacerbated, negative synergistic impact on bees.

To maintain healthy pollinator populations in modern agroecosystems, it is essential we understand the mechanisms through which land use change impacts bee populations. To address this question, we used a structural equation modeling framework to evaluate the direct, indirect, and interactive effects of 1) increasing agricultural habitat , 2) reduced floral diet diversity in bee-collected pollen, and 3) increased pesticide risk in bee pollen on female offspring number and weight in solitary mason bee O*smia cornifrons* Radozkowski (Hymenoptera: Megachilidae) populations in New York apple (*Malus domestica*; Rosales: Rosaceae) orchards during bloom.

We hypothesize that (Fig. 1):

Increasing agricultural habitat will reduce bee offspring number and weight 1) directly, through mechanisms not studied here (increased foraging trip time, parasitism, and/or predation), and also indirectly, by 2) decreasing diet diversity and/or increasing 3) pesticide risk levels in bee-collected pollen.

We also expect 4) reduced diet diversity will increase pesticide risk levels in bee collected pollen, because diets with a high proportion of mass-flowering apple pollen are more likely to be contaminated with agrochemicals. Finally, we expect 5) reduced diet diversity and increased pesticide risk levels in bee pollen will synergistically interact to reduce offspring number and weight as homogenous, low nutrient diets could hinder detoxification of pesticide-laden pollen.

Materials and Methods:

Study Design

Apple is an important crop for New York state and *O. cornifrons* is an apple pollinator (Maeta, 1990) that nests in trap nests and responds to stress in measurable ways (Tepedino & Torchio, 1982). Although recently introduced from Japan, non-native *O. cornifrons* shares characteristics with many native bee species in apple: it is solitary, univoltine, polylectic, and mass-provisioning (Bosch & Kemp, 2001). For our sites, we choose 17 privately owned apple orchard, at least 1 km apart in the Finger Lakes region of NY (Fig. 2). Orchards ranged from 0.358 to 58.504 hectares (measured in qGIS) and varied in proportion surrounding agriculture from 0.090 to 0.559 (Fig. 2, Fig. S4 in the Supporting Information) and agrochemical management, including organic, conventional and abandoned sites. Although we collected data throughout bee activity (see *Experimental Populations*), to accurately compare across sites, we assessed pesticide risk, diet diversity, and bee response at three time points per site that best encompassed the highest bee offspring production. This resulted in 51 observations per variable, some of which extended beyond apple bloom (see Table S4 for dates).

Landscape Composition

To test our hypotheses with agricultural habitat, we also included in our analysis all other habitats that might distinctly impact bees. We used ArcGIS [ArcMap 10.5.1] and the USDA 2015 Crop-Scape Data Layer to quantify the proportion of: agricultural, urban, open (wildflowers, grasslands, and pasture), forest, and shrub/wetland habitats surrounding bee nests. Indeed, urban gardens, open fields, forest trees, and shrubs and flowers in wetland habitats vary in resource abundance, bloom time, and functionality to bees. To find

the most explanatory habitat variables scales for each hypothesized relationship (Fig. 1), we measured landscape composition at eight radii surrounding our 17 sites (250, 500, 750, 1000, 1250, 1500, 1750, and 2000 m). The smallest scale is smaller than the 400 m radius at which all displaced *O. cornifrons* females reliably return to their nests (Kitamura & Maeta, 1969), and the largest scale corresponds with the 2000 m^2 surrounding patch sizes necessary to sustain high density of certain floral resources (Dauber et al., 2010). It is important to note that habitat variables were not independent of one another (see Results).

Experimental populations

Experimental bees were sourced from wild *O. cornifrons* populations by placing empty cardboard "trap-nest" nest tubes lined with paper (15.24 cm long by 7.5 mm diameter [crownbees.com]) at 6 privately-owned suburban backyards within the Town of Ithaca, NY (longitude: 42.428527 to 42.469463, latitude: -76.530422 to -76.465609 DD). We x-radiographed (Agfa DX-G CR, Sound-Eklin Mark 1114cw DR at 52 kVp and 3.2 mAs) source nest tubes to determine the number of adult bees per nest and then randomly assigned 20-22 tubes containing a total of 98 to 102 adult *O. cornifrons* bees (sex ratio averaged 59.4% female ± 2.3% standard error) per experimental site. At each site, we placed marked source nests tubes interspersed with 30-32 empty experimental nest tubes in a single wooden nest shelter erected within, or along the perimeter of, the apple orchard. To encourage nesting, we ensured that source nest tubes were placed in nesting shelters coinciding with apple bloom (May 5, 2015). Nesting shelters were protected from predation with Tree Tanglefoot® and chicken wire (Fig. S2). Average temperature between time points was calculated from hourly collections taken inside the mason bee nest shelters using data loggers [Embedded Data Systems iButtons].

From bee emergence (May 7) until offspring production ceased (June 24), we collected newly completed nest tubes every six days and replaced them with empty tubes, always maintaining vacant nest tubes. Of these observations, the three time points per site were chosen for analysis. If the total nest tubes produced at a time point were above 1 but below 10, then 1 nest tube was randomly selected for pollen analysis. When more than 10 nest tubes were produced, 2 to 4 were selected for pollen analysis. All other nest tubes were kept for offspring assessment (see nest tube numbers collected for each purpose in Table S4).

Offspring Response

Nest tubes collected for offspring analysis were stored, and protected in a shed (42.444329, -76.462235 DD) at ambient temperature and then moved (Nov 18) to a walk-in refrigerator on Cornell University campus for overwintering (3-4^{o}C). Starting on April 5 through April 20, 2016, bees emerged in 51 (one per time point), 23 cm^{3} collapsible mesh (mesh size < 1 mm^{2}) cages kept at ~20 ^{o}C on a 9/15 hr light/dark cycle. Non-target species (1.04% *O. lignaria* were identified through microscopy) were removed from our analyses. Across 6 years and 22 upstate NY apple orchards, less than 1 *O. corniforns* per orchard per year was collected in netting surveys (Russo, Park, Gibbs, & Danforth, 2015), making us confident that local bee establishment in experiment nest tubes was low.

Emerged offspring numbers were summed per time point and wet weight [Mettler Toledo MS105DU Semi-Micro Balance] was averaged for up to 10 males and 10 females (see Table S4) per time point. Due to two processing errors and three time points with no female emergence, there were only 46 observations for female weight. We chose female offspring number and female offspring weight as our response variables. Assessments of female offspring are more likely to reflect long-term population responses, because they produce offspring and provision nests. Additional analyses for the number and weight of male offspring, as well as the proportion of females, and larval mortality are included in Appendix S1.1, Fig. S1, and Table S1.

Pollen Analysis

Nest tubes set aside for pollen analysis were frozen (-20 ^{o}C) immediately, to preserve pesticide residues and to kill bee eggs before pollen was consumed. To assess diet diversity and pesticide risk, pollen homogenates were created per time point by combining an equal amount of pollen (within 0.05 g) from each nest tube, ensuring equal representation per individual adult female nest.

Pesticide Risk

We screened pollen homogenates for the active ingredients of 188 pesticides (Table S2 and Table S3), incorporating as many fruit crop pesticides as possible in one multi-residue liquid chromatography analysis.

We were unable to test for pyrethroids and chlorothalonil (common in agriculture), as well as mancozeb and captan (common apple fungicides) using liquid chromatography. Pesticides present in pollen were extracted using a modified version of the QuEChERS protocol (Stoner & Eitzer, 2013), analyzed with liquid chromatography/mass spectrometry/mass spectrometry (LC/MS/MS) and liquid chromatography/high resolution mass spectrometry (LC/HRMS). Detections were tested for quality using spiked samples. See Table S2 and Table S3 for quantitation limits. Pesticide risk was estimated as percent Hazard Quotient, or the summation of the amount in parts per billion (ppb) of each agrochemical detected in the mean pollen consumed per larval bee, in terms of its toxicity (LD_{50}) per bee. See equation modified from Stoner & Eitzer, (2013):

$$\%\ Hazard\ Quotient = \Sigma \frac{active\ ingredient\left(\frac{\mu g}{kg}\right) * \frac{pollen\ consumed\ (g)}{larva}}{LD50\left(\frac{\mu g}{bee}\right) * 1000} * 100$$

The mean pollen consumed per larva (186 ± 4 mg) was estimated from the average weight [Mettler Toledo AG245 Analytic Laboratory Scale] of the 994 provision masses (from 109 nest tubes) collected for pollen analysis. Because both larval and oral LD_{50} values and/or LD_{50} values specific to *O. cornifrons* were unavailable, we used acute (48 hr) topical LD_{50} value based on adult honey bees. Thus, we can use percent hazard quotient (%HQ) to compare bee risk across sites, but this metric cannot predict exact *O. cornifrons* larval mortality. To consistently estimate risk across pesticides and sites, we emulated a worst-case scenario, selecting the lowest determined LD_{50} values (EPA, 2018; IUPAC, 2017; Tomlin, 2009), or the next highest whole number of inexact (greater than a number) LD_{50} values. No LD_{50} value was available for 4-hydroxychlorothalonil, so we conservatively assumed substituted the LD_{50} of its parent chemical, chlorothalonil. Only fungicide and insecticide risk were estimated, as herbicide risk was low.

Diet Diversity

For each time point, we combined 24 to 25 mg homogenate pollen with 200 **µ**L of water and vortexed and sonicated the mixture until pollen was granularized. Ten **µ**L of the resulting solution was pipetted onto microscope slides with 38 to 40 **µ**L of Calberla's stain solution. Using an Olympus BX41 compound light

microscope at 40x magnification, we counted 300 pollen grains per slide that were completely within randomly-generated field-of-view transect(s), excluding grains with obviously broken exines. Pollen grain morphotypes composing more than 3% (9 grains) of the sample were identified to family level using pollen keys and image libraries (Kapp, Davis, & King, 2000; Russo, 2014), floral ranges and bloom times (USDA, 2017; Weldy, Werier, Nelson, Landry, & Campbell, 2017), and vouchered pollen slides collected from the environment surrounding our sites in 2014 (Appendix S1.2). We quantified pollen floral richness, diversity (Shannon Index), and evenness at the family level. In addition, we measured the proportion of the top four floral families collected in the pollen provisions (found at >10 sites): Vitaceae, Rhamnaceae, Rosaceae (most likely apple, see Fig. S3), and Caprifoliaceae.

Statistical Analysis

To evaluate our hypothesized relationships (Fig. 1) between habitat, diet diversity, pesticide risk, and female offspring and weight simultaneously, we adapted an information-theoretic approach (Burnham & Anderson, 2002) in two steps:

1) Variable selection:

In R, we used the dredge function (MuMln Package; Barton, 2018) to rank single predictor linear mixed effect models (lme function, nlme package; Pinheiro, Bates, DebRoy, & Sarkar, 2018) by the lowest corrected Akaike Information Criterion (AICc) value using maximum likelihood (Burnham & Anderson, 2002), and assuming linearity and normality. All models included site as a random variable. First, we selected the most explanatory predictor variable for all measures of habitat (Fig. 1:1), diet diversity (Fig. 1:2b), and pesticide risk (Fig. 1:3b), with female offspring number and weight as response variables. Next, we used the resulting diet diversity and pesticide risk variables as responses of all measures of habitat (see Appendix S2 for list of variables tested).

2) Confirmatory Path Analysis:

Using the selected variables (see Table S5) , we constructed two piece-wise structural equation (SEM) models (lme function, nlme package; Shipley, 2016) for: 1) female offspring number and 2) female offspring weight. Piece-wise SEM was chosen because it allows one to incorporate variables as both predictors and responses, and to account for random effects in the same analysis. Each path analysis was composed of the following two models: 1) bee response dependent on habitat, pesticide risk, diet diversity, and their

interaction term, 2) diet diversity dependent on habitat, 3) pesticide risk dependent on habitat. To minimize error, we included site as a random variable in all models, average temperature and time point as fixed variables in model 1, and the number of pollen provisions per homogenate as a fixed variable in models 2 and 3 (see Table S3 for temperature and pollen provisions per time point). We accounted for covariance between female offspring weight and pollen provision number by including the relationship as correlated error in both path analyses. Path model residuals were graphically inspected to ensure that there were no violations of normality and homoscedasticity, and responses with non-normal distributions (skew < -1.5 and > than 1.5, kurtosis > 3.5) were transformed. To correct positive skew and kurtosis, insecticide risk, fungicide risk, and proportion Roscaeae were log plus one, sixth-root, and square-root transformed, respectively. To correct negative skew, female weight was squared. Because female offspring was integer data, it was square-root transformed (Poisson and Quasi-poisson models were over-dispersed). Transformed models were tested for multicollinearity (VIF <4) and spatial autocorrelation (-0.103< r <0.076, p> 0.100) in the residuals using the Mantel test (ade4 package, Dray & Dufour, 2007).

To assess overall fit of path models, each independence claim was evaluated using Shipley's d-separation test and the resulting observed correlations were compared to random variation using Fisher's chi-square C-statistic (Shipley, 2016). Statistics for path models were calculated and fitted by maximum likelihood methods using the piecewiseSEM package (Lefcheck, 2017). Initial path models were consistent with the data (number of female offspring: Fischer's C=9.017, p=0.701, df=12; female offspring weight: Fischer's C=8.99, p=0.704, df=12), but model fit, in terms of AIC-, was improved (see Δ AIC in Fig. 3 caption) by iterative removal of non-significant (p>0.1) relationships (Shipley, 2013). We used 90% significance as our cut-off, to account for marginally significant, important relationships that could have indirect effects on downstream variables in our path model. We assessed robustness of results by: 1) measuring the change in effect size estimates and significance when replacing habitat variables in our final paths with adjacent scales, and 2) conducting Monte Carlo simulations on path analyses with low numbers of observations (Appendix S2). We used single-predictor, Pearson's models to test for relationships where correlation coefficients between habitat variables exceeded 0.5 at our largest (2 km) and smallest (250 m) scales. To test for a trade-off between female offspring weight and number and to test for a relationship between orchard size and proportion Rosaceae collected in pollen, we built additional linear models (site random, time point fixed) using ANOVA. Model normality and transformations were conducted as above. All analyses were conducted using R 3.4.2 (R Core Team, 2017).

Results:

Across sites, the habitats with the highest proportion coverage at a 2 km radius were forest (0.325 ± 0.042, n=17), followed by agricultural (0.266 ± 0.037, n=17), urban (0.132 ± 0.033, n=17), open (0.123 ± 0.009, n=17), and shrub/wetland (0.069 ± 0.006, n=17) habitat (Fig. 2; Fig. S4). Agricultural and urban habitats were positively correlated at 2 km and 250 m. There were additional positive correlations between agricultural and shrub/wetland and open and shrub/wetland habitats, as well as a negative correlation between agricultural and open habitats at 250 m. Of the 188 tested agrochemicals, 13 insecticides and 15 fungicides were found in the pollen provisions (see Table S2), ranging from 1.5 to 7,325.7 ppb (Table S6). In their pollen provisions, bees collected 11 floral families, averaging 3.14 (± 0.16, n=51) families per time point, and the top floral families included Vitaceae, Rosaceae, Caprifoliaceae, and Rhamnaceae (Fig. S5). On average, 22 female offspring emerged per time point weighing 57.43 ± 0.09 mg (n=46; Table S4). There was a strong positive correlation between orchard area and the proportion Rosaceae collected in pollen provisions ($F_{1,15}$=7.88, p=0.013, n=51; Fig. S3). We had expected an energetic trade-off between female offspring number and weight, but instead we found that the two variables were positively correlated ($F_{1,28}$=9.044, p=0.0055, n=46; Fig. S6). Permutations in habitat variable scales (Table S7) resulted in minimal changes to effect size (<0.009) and p-values. Monte Carlo simulations yielded relatively high (>0.742) chi-squared values, indicating that our path model results were robust (Appendix S2). Below we present the resulting best-fit path models (see Table 1 for path statistics) for both female offspring number (Fig. 3A) and female offspring weight (Fig. 3B) in terms of our hypotheses.

Agricultural habitat will reduce bee offspring number and weight directly and/or indirectly, by decreased diet diversity and/or increasing pesticide risk levels in pollen:

As the proportion agricultural habitat surrounding sites at 250 m increased, floral diet diversity in bee-collected pollen was reduced (Fig. 3A, Fig. 4A), which, in turn, resulted in fewer female offspring (Fig. 3A, Fig. 4B). Also as predicted, agricultural habitats at 2 km corresponded with increased insecticide risk levels (Fig. 4C), however these risk levels did not impact the number of female offspring produced (Fig. 3A).

In our female weight path, we found a direct, positive effect of proportion open habitat at 2 km on female offspring weight (Fig. 3B, 5A). We also found that increasing proportion agricultural habitat at 500 m indirectly resulted in marginally (0.05<p<0.1) lighter females via its positive effect on fungicide risk in pollen

provisions (Fig. 3B, 5A, 5D). Increasing shrubland and wetland habitat at 1250 m indirectly increased female offspring weight, by decreasing the proportion Rosaceae collected in bee pollen and its subsequent marginally ($0.05<p<0.1$) positive relationship with fungicide risk levels (Fig. 5C). Increased fungicide risk levels, in turn, had a marginally negative effect on female offspring weight (Fig. 3B, Fig. 5D)

Reduced diet diversity will result in increased pesticide risk levels in pollen, and these variables will synergistically reduce offspring number and weight:

In the female weight path, fungicide risk levels in pollen marginally ($0.05<p<0.1$) increased as diets became more dominated by Rosaceae (Fig. 5C). However, in the number of female offspring path, we found no relationship between floral diet diversity and insecticide risk levels in pollen (Fig. 3A). We found no evidence for synergistic effects between diet diversity and pesticide risk levels in pollen provisions, neither on female offspring number, nor weight.

Discussion:

Here, we show that solitary bees nesting in agroecosystems produced fewer and smaller offspring as surrounding agricultural habitat increased and as open and shrub/wetland habitats decreased. These effects were driven by reduced diet diversity and increased pesticide risk levels in pollen, and the marginally ($0.05<p<0.1$) positive relationship between them. Although we had expected that crop-dominated diets would have negative nutritional consequences on bee offspring, our results suggest that Rosaceae-heavy diets did not affect female weight on their own, but only indirectly, by increasing fungicide risk levels in pollen. Past research in apple shows that increased fungicide use can reduce bee species richness and abundance, and that this effect is exacerbated in agriculture-dominated landscapes (Park, Blitzer, Gibbs, Losey, & Danforth, 2015). Our results with *O. cornifrons* suggest that increasing agricultural habitats can reduce female offspring weight, which might drive reductions in population abundance over time (see Implications).

The marginally ($0.5<p<0.1$) positive relationship between proportion Rosaceae and fungicide risk in pollen provisions was likely driven by pesticides applications on apple. In fact, the proportion of Rosaceae in pollen increased as apple orchard area increased (Fig. S3), indicating that Rosaceae pollen collected by bees was likely apple. Even if Rosaceous pollens were not apple, they could be subject to apple agrochemical

sprays, as we found both cultivated (*Prunus* and *Fragaria*) and creeping Rosaceae plants (*Potentilla, Geum, Rubus,* and *Rosa)* in and around the orchards. Interestingly, shrubland and wetland habitat, and not agricultural habitat, was the top predictor of proportion Rosaceae collected in bee pollen provisions. Perhaps *Osmia* collected relative less Rosaceae pollen in sites where shrubland habitat was high because they prefer shrubland resources to what was likely mass-flowering crop pollen. All pollen types collected (beside Rosaceae) were determined to genus or species and 6 of the 11 types were identified as shrubland plants, including buckthorn, honeysuckle, dogwood, privet, viburnum, and walnut. Indeed, past work corroborates our findings, showing that *Osmia* collect relatively more Rosaceae pollen and produce smaller provisions as surrounding natural habitats become limited (Nagamitsu et al., 2017).

While fungicide risk levels in pollen responded to agricultural habitats at a 500 m radius, within our maximum 600 m radii orchard sizes, insecticide risk responded to agricultural habitats at 2 km, a scale much larger than the focal orchards. Past research with honey bees in NY apple orchards reflects our results here, as the majority of pesticide exposure in the pollen they collected came from insecticides sprayed outside the orchards or prior to bloom (McArt, Fersch, Milano, Truitt, & Böröczky, 2017). Importantly, we found that diet diversity was a stronger predictor of the number of female offspring produced than was insecticide risk. Perhaps these nutritional requirements are more impactful to bee health than are the negative effects of insecticides during apple bloom. Indeed, polylectic *Osmia* have been shown to rely on a mixture of floral resources to maintain stable protein content in pollen provisions (Lunau & Budde, 2007). However, it seems curious that such high insecticide risk levels (exceeding 100% of the LD_{50} at 8 of 51 time points), did not appear to affect female offspring number. One explanation could be because female eggs were laid before insecticide risk was high. Indeed, growers tend to spray more fungicides during apple bloom and switch to insecticides after bloom (Park et al., 2015), and mason bees provision female offspring earlier in the season than males. Our results support this idea, as insecticide risk in pollen increased as time point progressed (Fig. 3A), and we found a significant, negative effect of insecticide risk on the number of male offspring (Fig. S1). Because we homogenized pollen provisions per nest, we are unable to disentangle pollen risk levels and offspring sex.

Interestingly, the strongest predictor of the number of female offspring was increasing open habitats (Table 1), which was not mediated by either pesticide risk levels or pollen diet diversity. In a separate study, our offspring were screened for the common fungal pathogen: chalkbrood, or *Ascosphaera*. Incidence of

larval mortality due to *Ascosphaera* decreased as surrounding open habitat increased (Krichilsky et al., in prep). Perhaps the weight reductions we found here were the result of *Ascosphaera* infections that were not virulent enough to outright kill female offspring. Another possibility is that open areas might support higher floral resource abundance. High bloom densities have been shown to reduce adult female foraging trip time (Westphal et al., 2006), and reduce nest predation and parasitism (Goodell, 2003), both of which would translate to more and heavier offspring.

Study limitations:

Because conclusions based on path analyses are limited to the variables accounted for, it is important to note that the "effects" we found on female offspring weight and number could have been influenced by extraneous variables. For instance, although most of our top predictors clearly outranked other variables (change in AIC >3), floral diet diversity explained female offspring weight almost as well as did the top predictor, proportion Rosaceae, but was not accounted for in the path (see Table S5). In addition, habitat variables were not independent of one another. Agricultural and urban habitats were positively correlated with one another and negatively correlated with natural habitat variables, indicating that the patterns we saw here might be due to both agricultural and urban habitats, and not agriculture alone. If we had been able to screen for some of the common apple pesticides (see Methods), it is possible that fungicide and insecticide risk levels in pollen could have had more pronounced effects on female offspring weight and number than are documented here. Because we delayed bee release to coincide with apple bloom, natural *O. cornifrons* populations could have faced additional stress due to high pesticide exposure or low floral resource availability prior to bloom that we did not capture here. It is also possible that potential impacts on mason bee populations may in fact be even larger when we account for male, as well as female, offspring weight and number. Male offspring number and weight were also negatively impacted by agricultural habitat, increased pesticide risk, and decreased diet diversity (Fig S1). Even though *O. cornifrons* shares characteristics with many wild, solitary bees in apple, it is non-native with a stable population, while many of its native counterparts have narrower diet breadths, have smaller body sizes, and are currently in decline (Bartomeus et al., 2013). Thus, we suspect that the population response of this introduced, non-native species may be a conservative estimate of how native bees would respond to similar stress. Further research with additional

species in multiple cropping systems is imperative to inform management strategies for wild bees in agroecosystems.

Implications:

Our results with *O. cornifrons* suggest that we can support wild bees in apple by 1) converting agricultural habitats to natural habitats, 2) increasing floral resource diversity in the environment through wildflower plantings or reduced mowing, and 3) reducing fungicide risk through alternative pest control techniques. Because we could not count adult females in the field, finding fewer *O. cornifrons* offspring could result from: 1) reduced per capita offspring production, 2) direct adult female mortality, or 3) adult female dispersal to more favorable locations (Bosch & Kemp, 2001). Regardless of the mechanism, *O. cornifrons* populations, and thus their pollination services, were reduced in agricultural habitats. Not only did we find fewer female offspring as agricultural habitats increased and open and shrub/wetland habitats decreased, but they also weighed marginally ($0.05<p<0.1$) less. Reduced intra-specific female body size in bees can lead to decreased offspring production, slower provisioning rates, reduced longevity (Bosch & Vicens, 2006; Kim, 1997), and even less effective pollination services (Jauker et al., 2016). We must continue to research the simultaneous impacts of multiple variables on pollinator health in order to ensure that our important pollinator species are not unwittingly handicapped in the very environments where we rely on them.

Supporting Information:

Additional Supporting Information may be found in the online version of this article:

Authors' contributions:

MC, BD, and KP conceived ideas and designed the methodology; MC, MvD, BE, LR and NM collected data; MC, BE, LR, and NM analyzed data; MC, BD, and KP led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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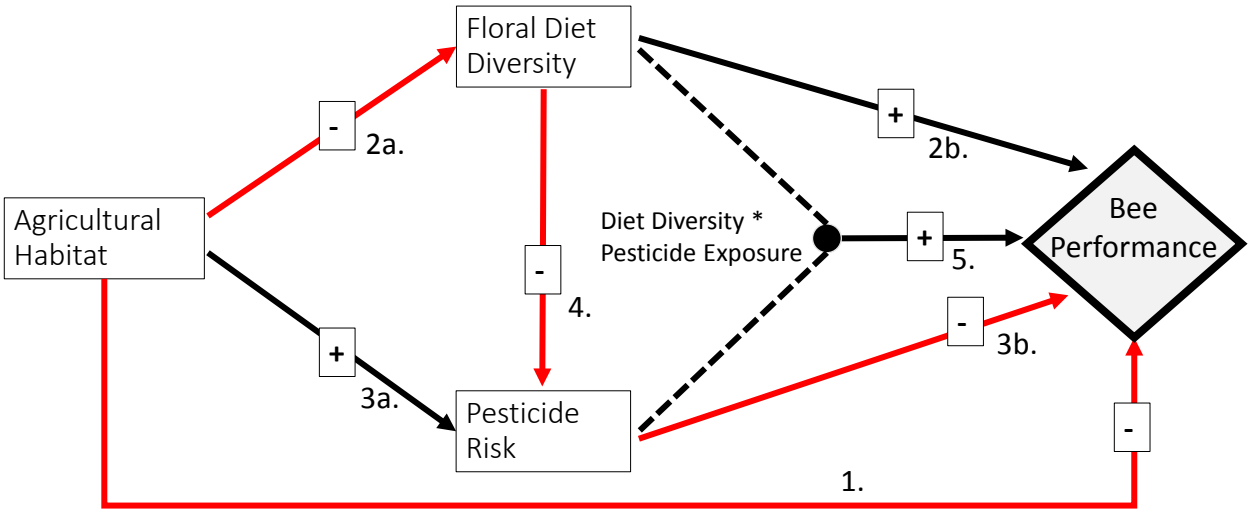

Figure 1: A schematic representation of our hypotheses (1-5). Increasing surrounding agricultural habitat will have a net negative effect on bee offspring number and weight directly (1), or indirectly via diet diversity (2a and 2b) and/or pesticide risk (3a and 3b), and/or their combined effects (4, 5). Arrows represent unidirectional relationships between variables in boxes. Red/black arrows labeled with minus/plus signs represent negative/positive relationships. Dashed lines and circle represent a multiplicative interaction. Numbers and letters correspond to the hypotheses in the Introduction, as well as the *Variable Selection* section of the Methods.

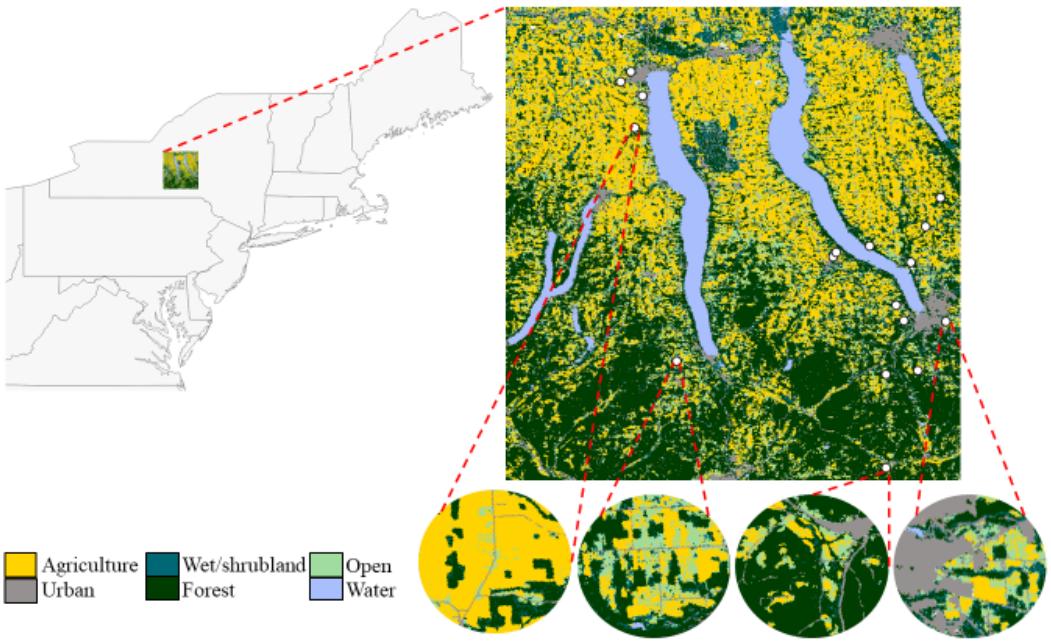

Figure 2: A map of upstate New York, showing the locations of the 17 orchard sites in our study. Geographic dimensions of the color insert are 83.516 by 106.355 km (40.06 to 42.96 DD N, -76.13 to -77.14 DD W). Map colors correspond with our 5 habitats, and also shows open water. The variation in landscape composition amongst 4 of our sites at is shown at a 2 km radius. See Fig. S4 for habitats coverage at all sites.

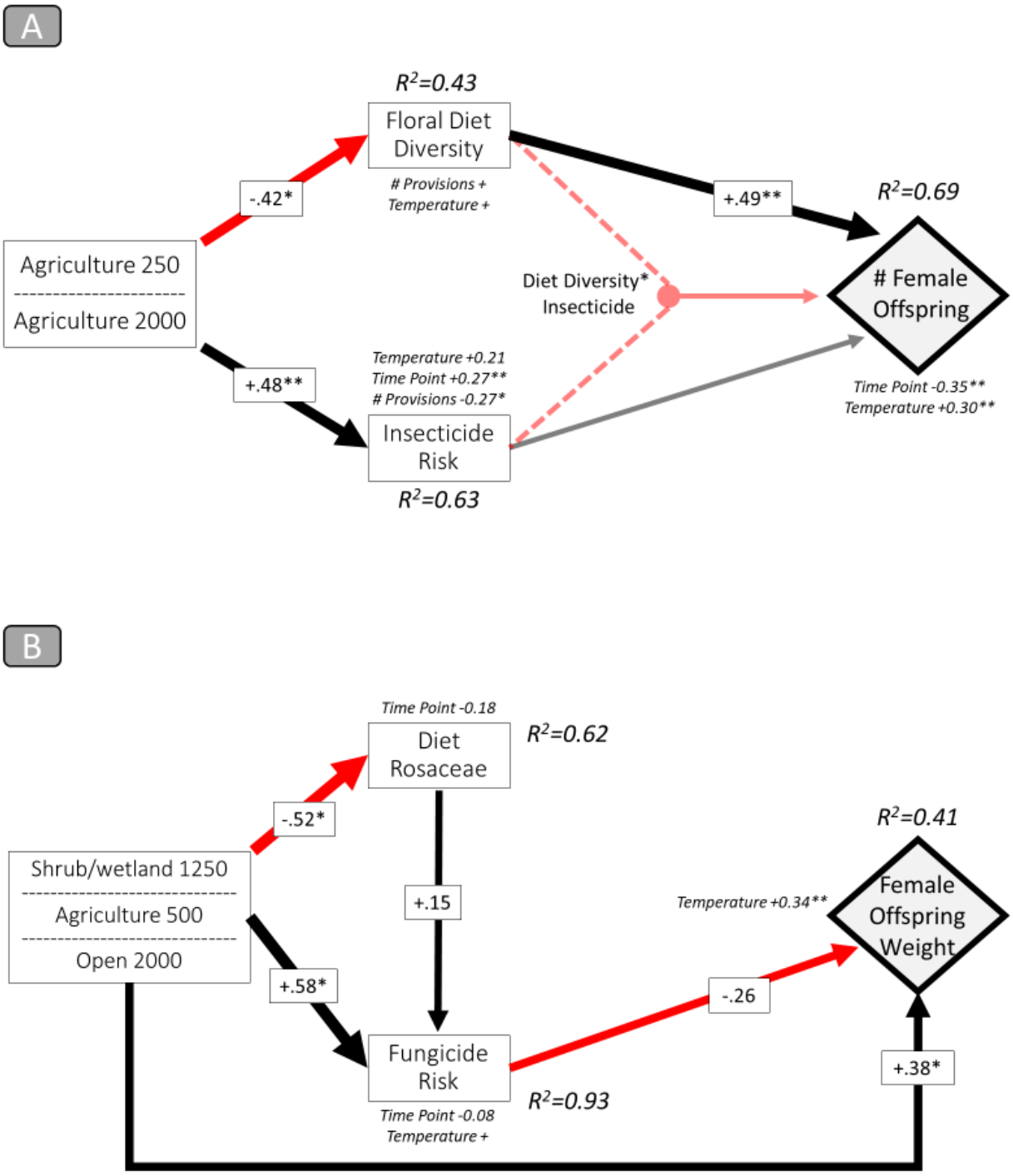

Figure 3: Resulting final path models for the number of female offspring (A; Fisher's C=7.956, p=0.789, df=12, n=51, Δ AIC from initial model=-7.061) and female offspring weight (B; Fisher's

C=14.813, p=0.675, df=18, n=46, Δ AIC =-6.177). Unidirectional arrows represent supported relationships (red negative, black positive) between variables (in boxes). Arrows are scaled to the magnitude of the standardized correlation coefficients, shown in boxes alongside arrows accompanying p-value significance levels (0.05<p<0.1=no symbol, 0.01<p<0.05=*, 0.001<p<0.01=**, p<0.001=***). Semi-transparent arrows represent non-significant (p>0.1) relationships that still support the model fit. Links found in a priori model may be omitted here because their removal increased model fit. For clarity, the variables “Number of Pollen Provisions” (# Provisions), “Temperature”, and “Time Point” have been omitted and instead their correlation coefficients, if significant, are included in italics next to their associated response variables. Numbers accompanying habitat variables represent the scale, or meter radius, about sites. Statistics are based on transformed variables (see Table 1).

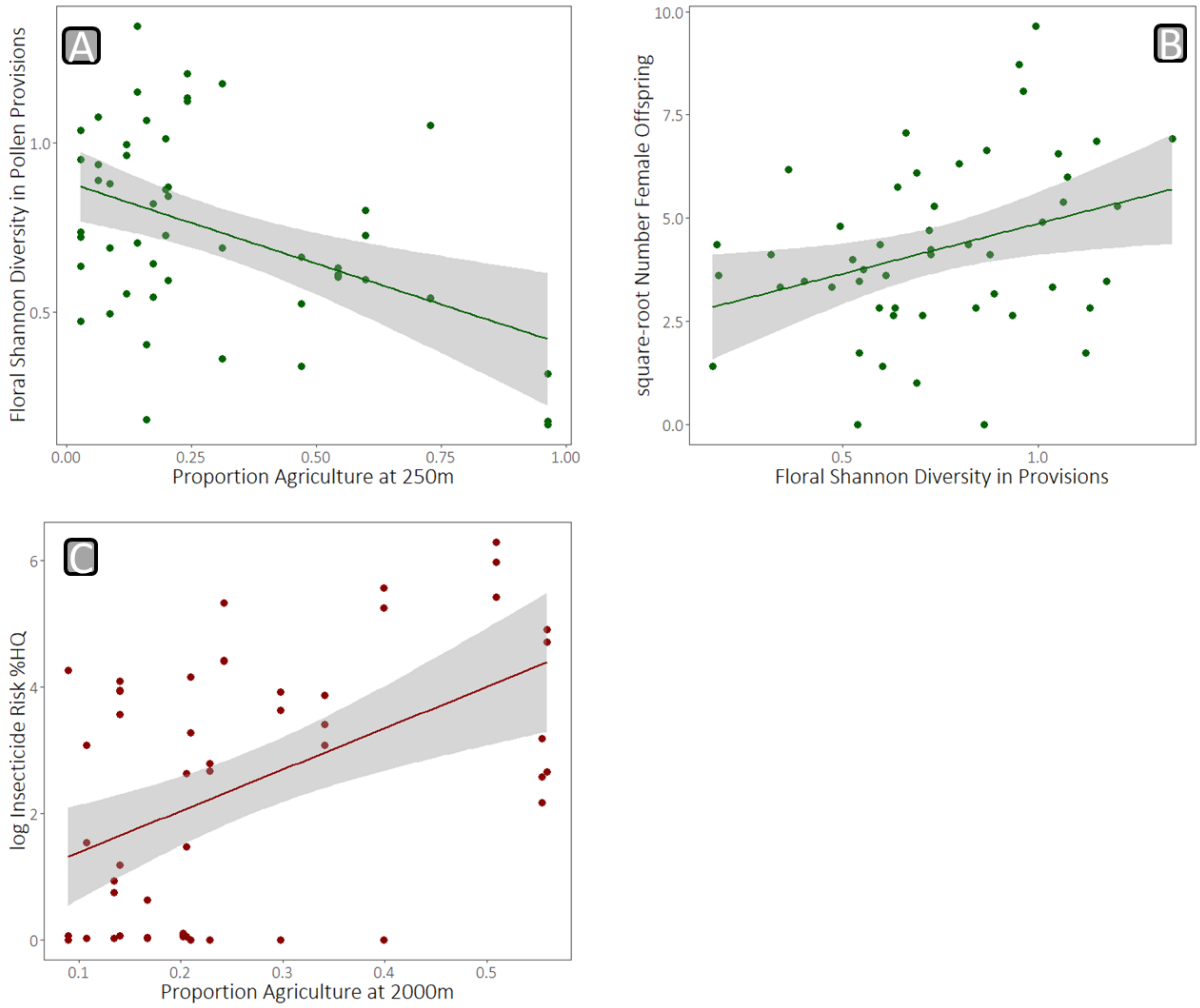

Figure 4: The three pairwise relationships suggested by the final number of female offspring path analysis. Here, we show the relationships between surrounding agricultural habitat at 250 m and floral diet diversity in bee-collected pollen provisions (A; p=0.017, n=51), between floral diet diversity and the number of female offspring produced (B; p=0.005, n=51), between agricultural habitat at 2000 m and insecticide risk levels (% hazard quotient) in pollen provisions (C, p=0.006, n=51). Points denote time-point observations, lines relationships between variables, and grey shadows 95% confidence intervals. Plots account for variable transformation, but not random variables (See Table 1 for multi-modal SEM statistics).

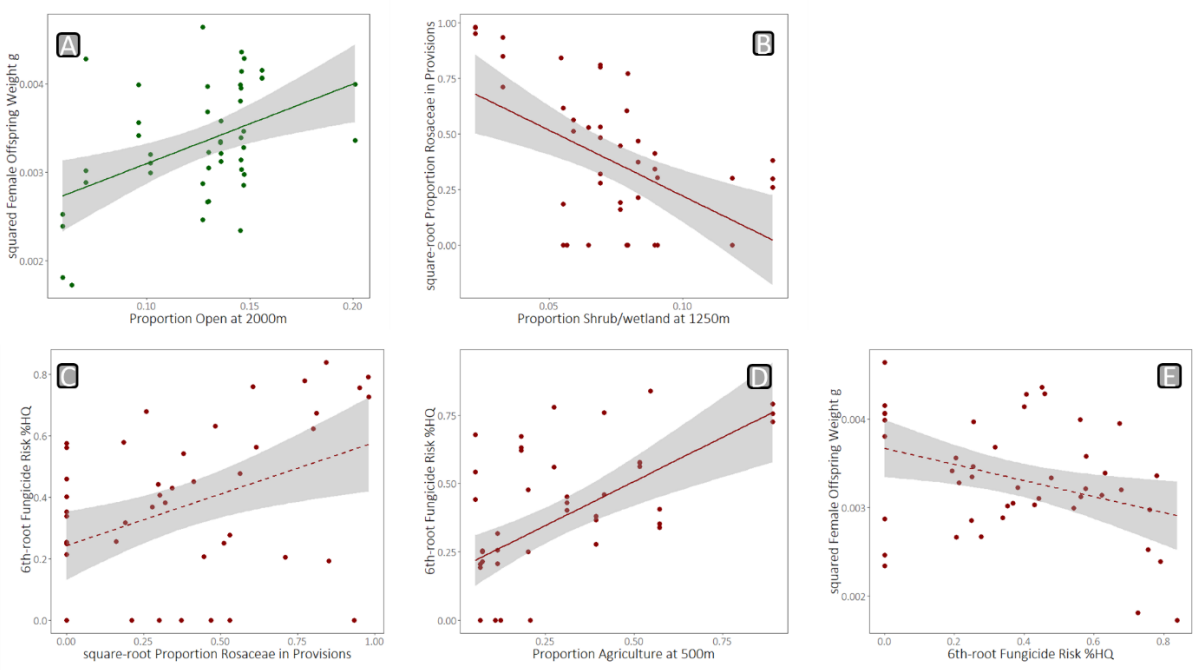

Figure 5: The pairwise relationships suggested in the final path analysis for female offspring weight, including the relationships between open habitat at 2000 m and female offspring weight (A; p=0.010, n=46), between shrub/wetland habitat at 1250 m and proportion Rosaceae in bee-collected pollen provisions (B; 0.011, n=46), between proportion Rosaceae and fungicide risk levels in pollen (C; p=0.069, n=46), between agricultural habitat at 500 m and fungicide risk levels in pollen (D; p=0.011, n=46), and between fungicide risk levels and female offspring weight (E; p=0.052, n=46). Points show time-point observations, solid lines denote significant ($p<0.05$), dotted lines marginal ($0.05<p<0.01$), relationships between variables, and grey shadows represent 95% confidence intervals. Plots show single predictor data with no random variables (See Table 1 for multi-modal SEM statistics).

Table 1: SEM analysis statistics for each bivariate relationship in the final structural equation models for the number of female offspring and female offspring weight. The response and predictor variables are listed along with their correlation coefficients, standard errors (se), degrees of freedom (df), sample size (n), critical values, p-values, significance levels, and transformations (response variables are listed first followed by predictor variables in order of appearance). Significance symbology is as follows: $0.05<p<0.1$=no symbol, $0.01<p<0.05$=*, $0.001<p<0.01$=**, $p<0.001$=***. Variables in italics represent correlated errors.

SEM Model	Response	Predictor	se	df	n	Critical Value	p-value	Correlation Coefficient	Significance	Transformation(s)
Number Female Offspring	Insecticide Risk (%HQ)	Agriculture 2000 m	1.999	15	51	3.203	0.006	0.480	**	log+1
	Insecticide Risk (%HQ)	Time Point	0.224	31	51	2.904	0.007	0.266	**	log+1
	Insecticide Risk (%HQ)	Temperature	0.059	31	51	1.867	0.071	0.206		log+1
	Insecticide Risk (%HQ)	Number Pollen Provisions	0.032	31	51	-2.534	0.017	-0.274	*	log+1
	Floral Shannon Diversity	Agriculture 250 m	0.166	15	51	-2.680	0.017	-0.417	*	
	Floral Shannon Diversity	Temperature	0.010	32	51	0.982	0.333	0.128		
	Floral Shannon Diversity	Number Pollen Provisions	0.005	32	51	1.196	0.240	0.156		
	Number Female Offspring	Floral Shannon Diversity	1.170	29	51	3.049	0.005	0.486	**	square-root
	Number Female Offspring	Insecticide Risk (%HQ)	0.313	29	51	0.025	0.980	0.008		square-root, log+1
	Number Female Offspring	Time Point	0.247	29	51	-3.559	0.001	-0.349	**	square-root
	Number Female Offspring	Temperature	0.053	29	51	3.128	0.004	0.300	**	square-root
	Number Female Offspring	Floral Shannon Diversity: Insecticide Risk (%HQ)	0.405	29	51	-1.359	0.185	-0.393		square-root, log+1
	Number Female Offspring	*Number Pollen Provisions*	*NA*	*51*	*51*	*2.602*	*0.006*	*0.352*	***	*square-root*

Table 1 Cont.

SEM Model	Response	Predictor	se	d.f.	n	Critical Value	p-value	Correlation Coefficient	Significance	Transformation(s)
Female Offspring Weight	Female Offspring Weight	Fungicide Risk (%HQ)	0.000	27	46	-2.032	0.052	-0.261		squared, 6th-root
	Female Offspring Weight	Open 2000 m	0.003	15	46	2.926	0.010	0.376	*	squared
	Female Offspring Weight	Temperature	0.000	27	46	2.866	0.008	0.342	**	squared
	Fungicide Risk (%HQ)	Proportion Rosaceae	0.063	26	46	1.895	0.069	0.146		6th-root, square-root
	Fungicide Risk (%HQ)	Agriculture 500m	0.226	15	46	2.921	0.011	0.585	*	6th-root
	Fungicide Risk (%HQ)	Temperature	0.003	26	46	1.638	0.114	0.075		6th-root
	Fungicide Risk (%HQ)	Time Point	0.014	26	46	-1.903	0.068	-0.084		6th-root
	Proportion Rosaceae	Shrub/wetland 1250 m	2.058	15	46	-2.904	0.011	-0.516	*	square-root
	Proportion Rosaceae	Time Point	0.038	28	46	-1.857	0.074	-0.178		square-root
	Female Offspring Weight	*Number Pollen Provisions*	*NA*	*46*	*46*	*0.675*	*0.252*	*0.102*		*squared*