

**Introduction:**

In recent decades there has been a lot of concern shown over the apparent decline of wild pollinating insects, and potential impacts on the ecosystem services they provide, especially in the industrialized societies of the northern temperate zone (e.g.[1–3]). Research attempting to measure the presence and magnitude of these declines has taken several approaches. The most common approaches to long-term trend detection utilize large public databases of amalgamated observation data from a wide range of sources, including citizen science projects and institutional collections (e.g.[4–7]). More recently several authors have used occupancy modelling to generate fine-grain spatial estimations of decline [8,9] from similar datasets. However, due to the diverse protocols and uneven sampling effort over time and space that gave rise to these data, such studies have primarily focused on a subset of pollinator community metrics, such as richness, diversity, and relative abundance, which are more readily assessed with heterogeneous data. Abundance and visitation, the community metrics that are most directly pertinent to estimating ecosystem services and function, are difficult to estimate from these sorts of data [10].

Despite widespread acknowledgement of the need for long-term monitoring of pollinator abundances in North America [11] and abroad (e.g. [12]), very few such studies have been carried out. Published time-series on abundances of pollinating insect groups are dominated by studies of butterflies and other lepidoptera [13], with a few on syrphid flies [14–16]. These studies have produced mixed results, with both the magnitude and direction of trends differing between regions and taxa [13,17]. Meanwhile, there have been only a few multi-year studies on the abundance of the most functionally important pollinator taxa in temperate ecosystems: bees [18–20].

A search of the literature found only two 21<sup>st</sup> century studies on trends in bee abundance in North America that included 5 or more years of monitoring data. Onuferko et al. [21] conducted a long-term study of the reestablishment of bee communities in a reclaimed site in Ontario, Canada, from 2003-2013. During the course of that study, they incidentally measured a significant decline in bee capture rates at their control sites, outside of the focal restoration zone. Kammerer et al. [22] recently published an analysis of 10 years of trap data from the US mid-Atlantic region. While the paper did not emphasize overall trends in abundance for the region, they did find that climatic and weather variables associated with anthropogenic climate change were predictive of local declines in abundance of several bee taxa. Long-term monitoring of rates of bee visitation at flowers is similarly lacking. Carlos Herrera's 2019 [23] monograph on visitation of several pollinator groups to 65 plant species in the remote hills of southern Spain stands alone as a recent study of longer-term trends in pollinator visitation rates to plants.

In light of the dearth of published information on trends in bee abundance and bee visitation rates to flowers, it is difficult to say whether the ecosystem services provided by bees are declining. Given the widespread societal concern surrounding the pollinator decline hypothesis, I find this lack of monitoring data surprising. Fortunately, the Winfree Lab has been collecting data on regional crop visitation for over a decade, including data on watermelon, blueberry, and cranberry systems. I decided to analyze 6 years of visitation data collected at watermelon farms in New Jersey and Pennsylvania, over 8 years from 2005 to 2012, to see whether there were any detectable trends in the rate of bee visitation to flowers.

**Methods:****Study System:**

Watermelons (*Citrullus lanatus*) are an economically important crop grown worldwide that depend on invertebrate pollination to produce fruit. It is dioecious, meaning it has male and female flowers on separate plants, and requires hundreds to thousands of pollen grains to be deposited on stigmas in each female flower to produce fruit of marketable quality [24]. Focusing on a single pollinator-dependent plant species that is grown at consistent densities and field extents from year to year mitigates several potential sources of bias and noise in visitation rate data. For example, at the local scale bees have been shown to prioritize patches with high total resource density relative to neighboring patches [25], and individuals of many bee species exhibit floral constancy, preferentially visiting one or a few plant species of high relative abundance [26]. In natural systems interannual fluctuations in patch resource density and relative abundance of focal flora would have to be accounted for, which is no mean feat. The study is further strengthened by having a consistent sampling protocol across the entire time series.

#### The Data:

To measure pollinator visitation rate at flowers, a 50-m crop-row transect was established within each of 24 watermelon farms. Data were collected during the peak bloom of watermelon at each farm, between the 20<sup>th</sup> of June and the 20<sup>th</sup> of August each year from 2004-2012, except for 2006 and 2009 when no fieldwork was conducted. All farms were situated within a 90 by 60 km region of central New Jersey and eastern Pennsylvania, USA. Observational transects were carried out at each of the included farms on two separate days in 2005, on one day at each farm in 2007 and 2008, and on three days at each farm in 2010, 2011, and 2012. Pollinator visitation rate to flowers was calculated by conducting 45 second surveys of groups of flowers at 40 equally spaced points along each transect. At each point, the team observed all visits to as many flowers as they could confidently observe simultaneously. Each transect was sampled three times per day between 8:00 hours and 13:00 hours, which is the period during which watermelon flowers are open. Flower visitation rate data were recorded in units of pollinator visits per flower per unit time. Data was not collected when it was rainy, or when wind speeds exceeded 4.6 m/s. In the field, team members recorded all pollinator visits to flowers and visually identified each individual pollinator to one of twelve species groups. After collecting the flower visitation rate data, they collected voucher specimens of bees from watermelon flowers with hand nets for 30 min to be used for species identification and training.

#### Exploring the Data:

Not all farms were surveyed in all years. I decided to only use farms that had been visited in at least 4 of the 6 years for my analyses. This criterium made 5 sites ineligible and left me with 19 sites to include. I also excluded data from a 2004 pilot season which was collected under a different protocol (1 transect per day, rather than 3).

I grouped bees in 5 different ways for analyses: All bees, honeybees (*Apis mellifera*), all wild bees, bumblebees (*Bombus sp.*), and all bees other than honeybees and bumblebees. These groupings made sense ecologically and taxonomically while still maintaining sample sizes large enough to ensure model fitting algorithms converged successfully. In the late 1990s feral colonies of honeybees in North America were decimated by introduced parasites and pathogens [27] and were still rare during the period of this study. It is therefore likely that most visits by honeybees were by individuals from managed hives introduced to the fields by farmers to boost pollination services. I therefore also considered wild bees as group separately, as the response variable most representative of the full scope of natural ecosystem services being provided. Among wild bees, *Bombus sp.* are notable for their abundance (generally, as well as at watermelon flowers specifically), large size, high efficacy as pollinators (e.g.[28]), eusocial behavior,

and notable declines and shifts in relative abundance over the last century [7,8]. The remaining wild bee taxa were only modelled as a single combined group, because 1) the object of primary interest in this study is total ecosystem service provision, and 2) further division resulted in small datasets which gave convergence errors or failed to converge when models were run in R (R Team 2014).

To explore the relationship between year and visitation rate I summed the counts of visits per 30-minute transect, and because every visit to a farm included 3 transects spread similarly throughout the daily flowering period, I summed those three transects to get a total count of visits for a given site on a given day. I then considered two different approaches to handling the response variable in models of visitation rate over time:

1. Dividing the total number of visits by pollinators to flowers by the number of 45 second flower observations on that site-day transforms the visitation response variable to units of visits per flower per 45 seconds. This could then be assessed directly against predictor variables, including year.
2. Keeping the sum count of flower visits for a given site-day as the response variable and controlling for the variance in sampling effort (# of 45 second flower observations) in some other way.

Using the `fitdistrplus` package in R[30], I found that the raw, unfit visit rate data (approach #1) was well approximated by a gamma error distribution. The unfit visit count data (approach #2) was a good fit for a negative binomial error distribution (see Figures 1 & 2).

#### Selecting an error distribution family:

The ideal error distribution for modelling an effect is the one that best describes the distribution of the data around the predicted mean at each value of the predictor variables, rather than the distribution of the data around the overall mean of the response variable. Therefore, one must fit models and look at the model residuals to correctly determine the most appropriate error distribution.

I chose to use the maximum complexity model structure, amongst those under consideration, to compare error distribution fits. The only independent variable considered in this study will be year. While any relationship between year and pollinator visitation rate is attributable various other factors, such as inter-annual variations in weather, pesticide applications, or landscape use, the question being asked here is not so much about the mechanism of change but the sign and magnitude of it. Due to the nested structure of the data (multiple site-days each at several farms) and the unknown relationship between site-specific factors and visitation rate, including farm as a random effect will be considered. It seems reasonable that the direction of temporal trends in pollinator visitation may differ at sites spread across a 5,400km<sup>2</sup> area, so the maximum complexity model considered includes farm as a random intercept and random slope factor:

$$y_{ij} = \alpha_j + \beta_j(year) + \varepsilon_i$$

Where  $y_{ij}$  = number of visits per 45 second flower observation on site-day  $i$  at farm  $j$ ,  $\alpha_j$  is the farm specific rate of visitation at farm  $j$  in year 0, and  $\beta_j$  is the specific slope describing the relationship between year and visitation at farm  $j$ .

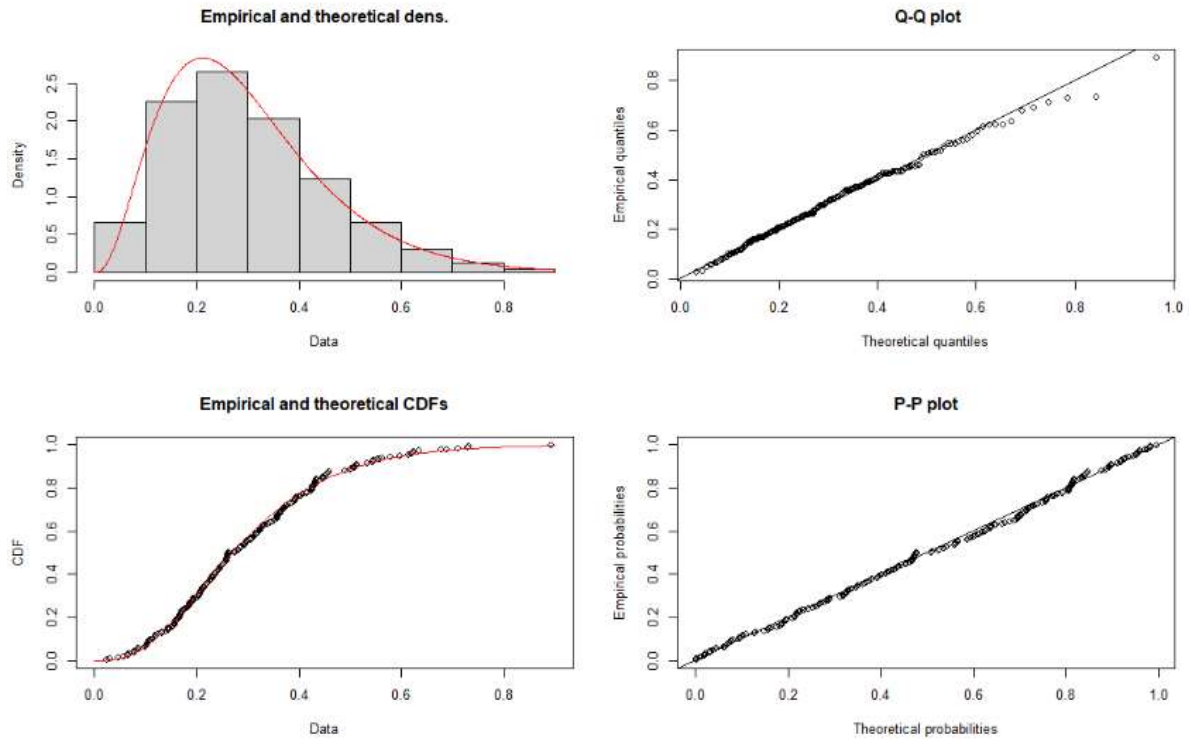


Figure 1: Comparisons of actual and theoretical distributions of raw data for a gamma distribution, with empirical count data converted to units of observations per flower per 45 seconds (rate). Produced using the ‘fitdistrplus’ package in R [30].

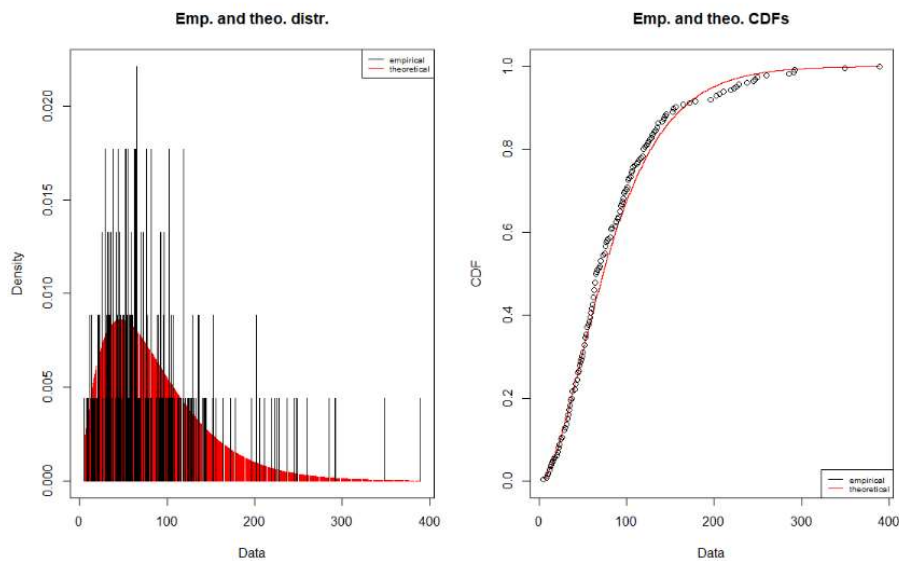


Figure 2: Comparisons of actual and theoretical distribution of raw count data for a negative binomial distribution. Produced using the ‘fitdistrplus’ package in R [30].

I initially attempted to run the models using the ‘glmer’ function from the ‘lme4’ package in R[31], with a gamma error distribution and log link. The model ran when considering the whole dataset of all bee visits. However, any subdivision into groups (e.g. *Bombus* only, or wild bees) introduced at least one 0 into the output variable set. In other words, while there were no site-days with 0 pollinator visits, there were site-days with visits by only wild pollinators, or only *Apis mellifera*. The gamma distribution does not allow for 0 values, and the models failed to run for bee subgroups. Because assessing the changes in sub-taxa visitation is of significant interest in this study, I decided to abandon this approach.

The alternative approach was to treat the number of pollinator visits as count data. Because all site-days had the same number of transects spaced similarly through the day, I summed all the recorded visits in a day for a site-day level count. The logical error distribution families for count data are the negative binomial family, including the Poisson and quasi-Poisson. The difference between each is in how the variance relates to the mean, with Poisson, quasi-Poisson, and negative binomial assuming a fixed (mean = variance), linear, and quadratic relationship, respectively. In order to compare which of these error distributions best fit the data, I fit models similar to the one above, with  $y_i$  now representing the total number of bee visits to flowers on site-day  $i$ . To compare the negative binomial family error distribution options, I fit models with the ‘glmmTMB’ function from the package of the same name in R on the ‘all bees’ dataset and compared the resulting distributions of residuals using the DHARMA package in R [32,33]. (Figure 3)

One would expect for the quasi-Poisson and negative binomial model residuals to show lower homogeneity and better fit than the classic Poisson in most cases, because they are of the same family but include additional parameters that increase the flexibility of the shape of the distribution. Indeed, the QQ plots of the residuals for the models tested are clearly much better for the negative binomial and quasi-Poisson, as were the results of the Levene Test for homogeneity of variance (Figure 3). The residuals conformed slightly better to expected values for the negative binomial than for the quasi-Poisson.

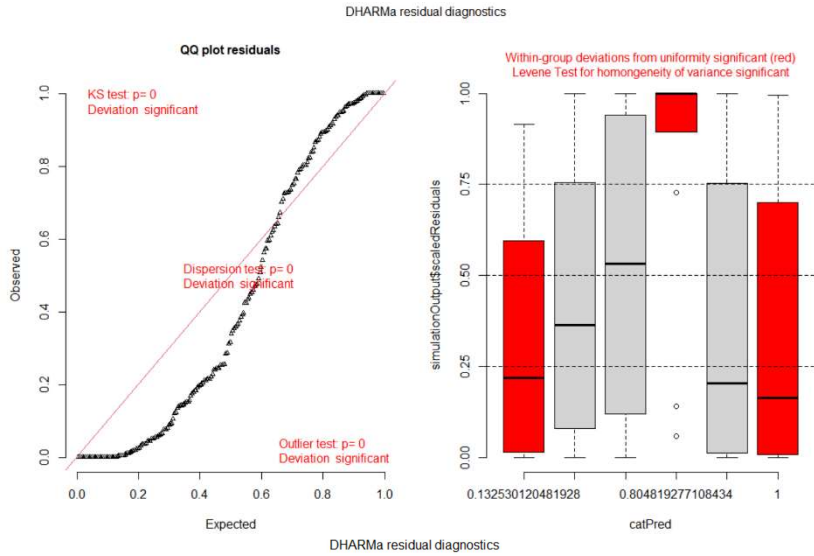
To compare AIC’s for negative binomial and Poisson error distributions, the same models were run using the ‘glmer’ and ‘glmer.nb’ functions from the lme4 package. The negative binomial model had a far lower AIC than the Poisson.

*Table 1: Comparison of AIC for the full complexity model using two different error distributions from the negative binomial family*

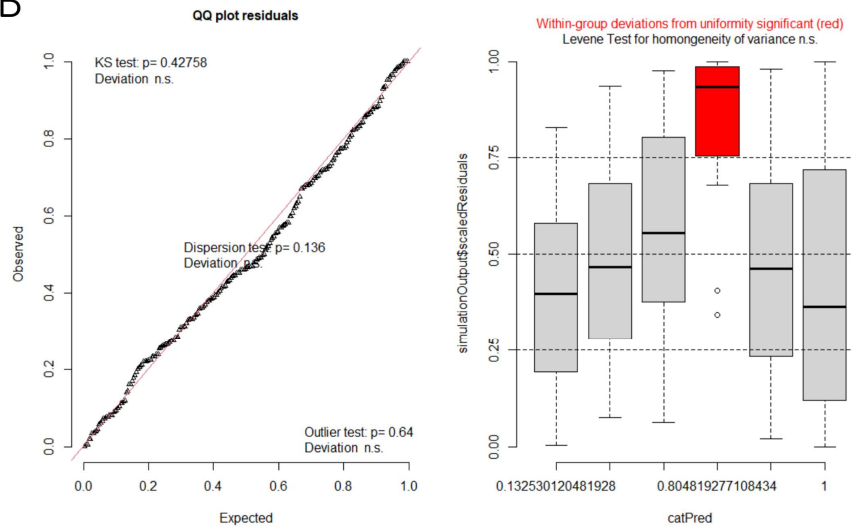
Error Distribution	Degrees of freedom	AIC
Poisson	5	6813.335
Negative Binomial	6	2338.801

Using the negative binomial or quasi-poisson error distributions are clearly the better choices. As they were a similarly decent fit for the data, I chose to continue with the negative binomial distribution. So far, the models have not accounted for different total observation times at different site-days, which has the potential to bias the results. Fortunately, there exists a convenient method for managing unequal sampling effort in negative binomial modelling.

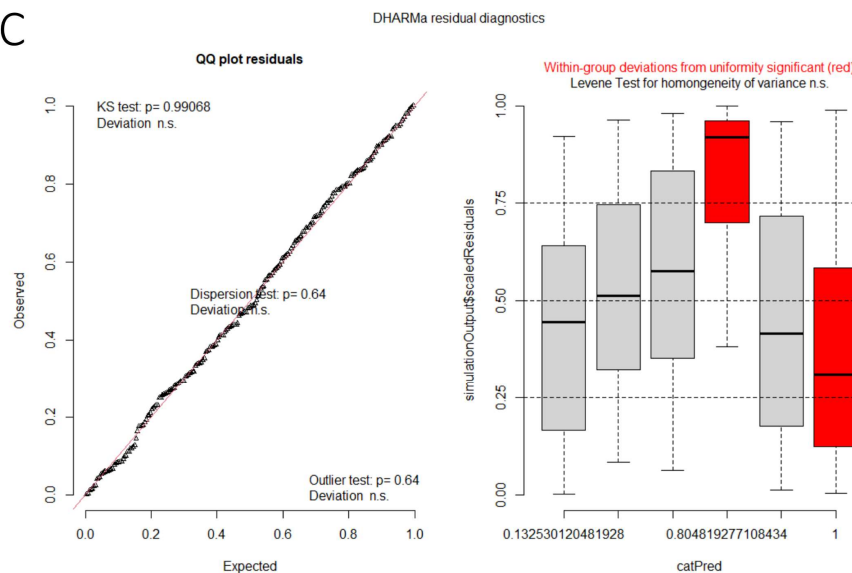
A



B



C



**Figure 3:** Comparison of residuals for maximum complexity models with different error distributions from the negative binomial error distribution family. A: Poisson, B: Quasi-Poisson, C: Negative Binomial. All models were generated using the 'glmmTMB' package, plots generated using the 'DHARMA' package

### Sampling Effort as an Offset:

A negative binomial distribution is a special case of the Poisson distribution where the variance isn't held equal to the mean. So, the model structure is the same as the standard Poisson regression:

$$\ln(E(Y)) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots \beta_i X_i$$

Where  $E(Y)$  is the expected value for the outcome variable given a range of parameters  $X_1$  through  $X_i$ , and  $\beta_0$  is the mean value of  $Y$  when all  $X$ 's = 0. In my case there is only one predictor of interest:

$$\ln(E(Y)) = \beta_0 + \beta_1 X_1$$

Where:

$Y$  = # of visits observed in a round

$X_1$  = year (2005 set = 0, so as to produce a meaningful intercept)

Removing the log by setting both sides to base  $e$ :

$$E(Y) = e^{\beta_0} * e^{\beta_1 X_1}$$

If we accept an assumption that doubling the number of flowers observed should double the number of visits observed, we can make number of flowers observed an 'offset' by adding it as a new variable  $Z$ , with a fixed coefficient of 1.  $Z$  is the natural log of the number of flowers observed, for reasons that will soon become apparent:

$$\ln(E(Y)) = \beta_0 + \beta_1 X_1 + 1 * Z$$

Where  $Z = \ln(\text{flowers})$ . If we raise both sides to  $e$ :

$$E(Y) = e^{\beta_0} * e^{\beta_1 X_1} * e^{\ln(\text{flowers})}$$

$$\frac{E(Y)}{\text{flowers}} = e^{\beta_0 + \beta_1 X_1}$$

We again have a model equation with expected visits per flower observation on the left-hand side, while also accounting for levels of sampling intensity. Because it uses the negative binomial error distribution, it can now accept 0's in the response variable, unlike a gamma distribution.

### Refining model structure; random effects:

Given that we have not made any assumptions or inferences on the spatial scale or site specificity of factors that might lead to inter-annual changes in bee abundance, it sounds reasonable to allow both the initial level and the trajectory of the relationship between year and visit-count to differ between farms. I compared the fits of models with various random effect structures for each bee grouping, using the negative binomial error distribution with the log of flowers observed as an offset. Table 2 shows Akaike Information Criteria (AIC) for each model, as well as an indication of whether the modelling functions encountered any convergence errors in the fitting process.

AIC comparison suggests that the random slope models consistently outperform the models with no random effect by a large margin, and that allowing farms to have a random slope does not improve model performance. P-values for the random slope elements were never significant, even when adjusted for testing on the boundary.

Table 2: Lowest AIC values for each bee group in bold. Type I error: Model failed to converge with max|grad|. Type 2 error: Fit is singular.

Bee Group	No Random Effect		Random Intercept		Random Slope + Intercept	
	AIC	Fitting Errors	AIC	Fitting Errors	AIC	Fitting Errors
All Bees	2268.5		<b>2260.2</b>		2263.3	
Honeybees	2032.5		<b>2025.0</b>		2027.8	I
Bumblebees	1602.3		<b>1580.1</b>		1582.1	I
All Wild Bees	2160.3		<b>2153.2</b>		2157.1	
Other	2020.0		<b>2004.7</b>		2008.5	I, II

## RESULTS:

The dataset included 19,726 individual visits by insect pollinators to watermelon flowers. Of these, 8022 (about 40%) were visits by honeybees. In the north-eastern US, feral colonies of honeybees are now rare due to introduced parasites and pathogens, so the majority of visits by honeybees were probably from managed hives introduced to the fields by farmers for pollination services. Amongst wild pollinators, bumblebees (*Bombus spp.*) were the most frequent visitors, with 3,528 visits (18%). Butterflies and syrphid flies only accounted for 151 (0.7%) and 493 (2.5%) visits, respectively. The remainder of recorded visits (7532, 38%) were by other wild bee species. Because they were relatively rare visitors, and they deposited little pollen per visit (unpublished data), non-bees were excluded from models and analyses.

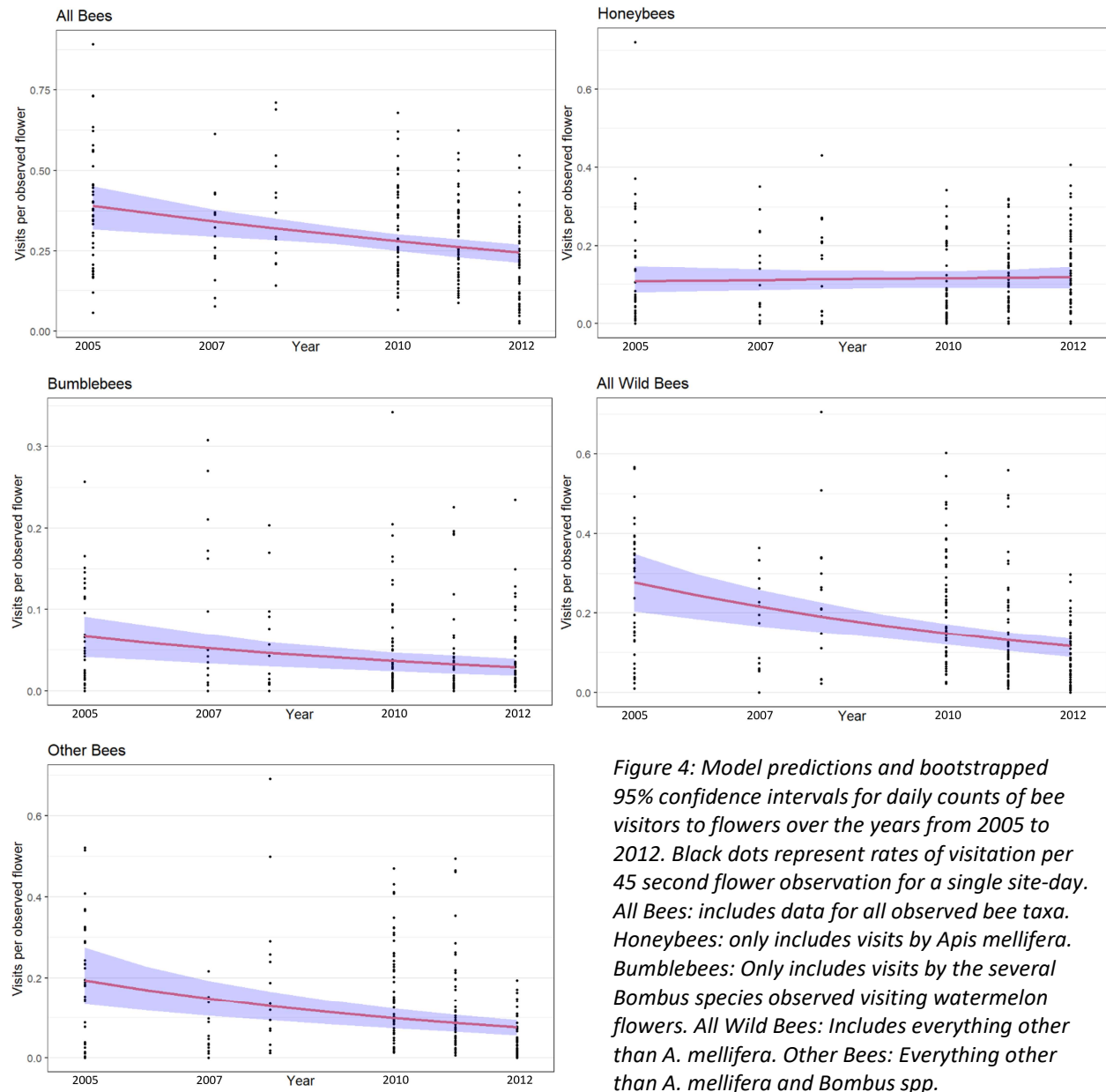
Overall, visits to watermelon flowers by all bees, managed and wild, declined over the period from 2005 to 2012 by 33%. This was driven primarily by a decrease in the rate of visitation by wild bees, which declined by 58% ( $p \leq 0.001$ ). In contrast, visits by honeybees show no clear trend (increase of 8%,  $p = .64$ ). A large decline was found in the visitation rate of bumblebees, which declined by 56% ( $p < 0.001$ ). Visitation by wild bees other than *Bombus* showed a decline of 61% over the period ( $p \leq 0.001$ ). The smaller variation in visit-rate by honeybees may reflect consistent stocking strategies by farmers, effectively smoothing some of the inter-annual variation in pollination service rendered. See Figure 4 for plots of visitation rate over time for each group[34].

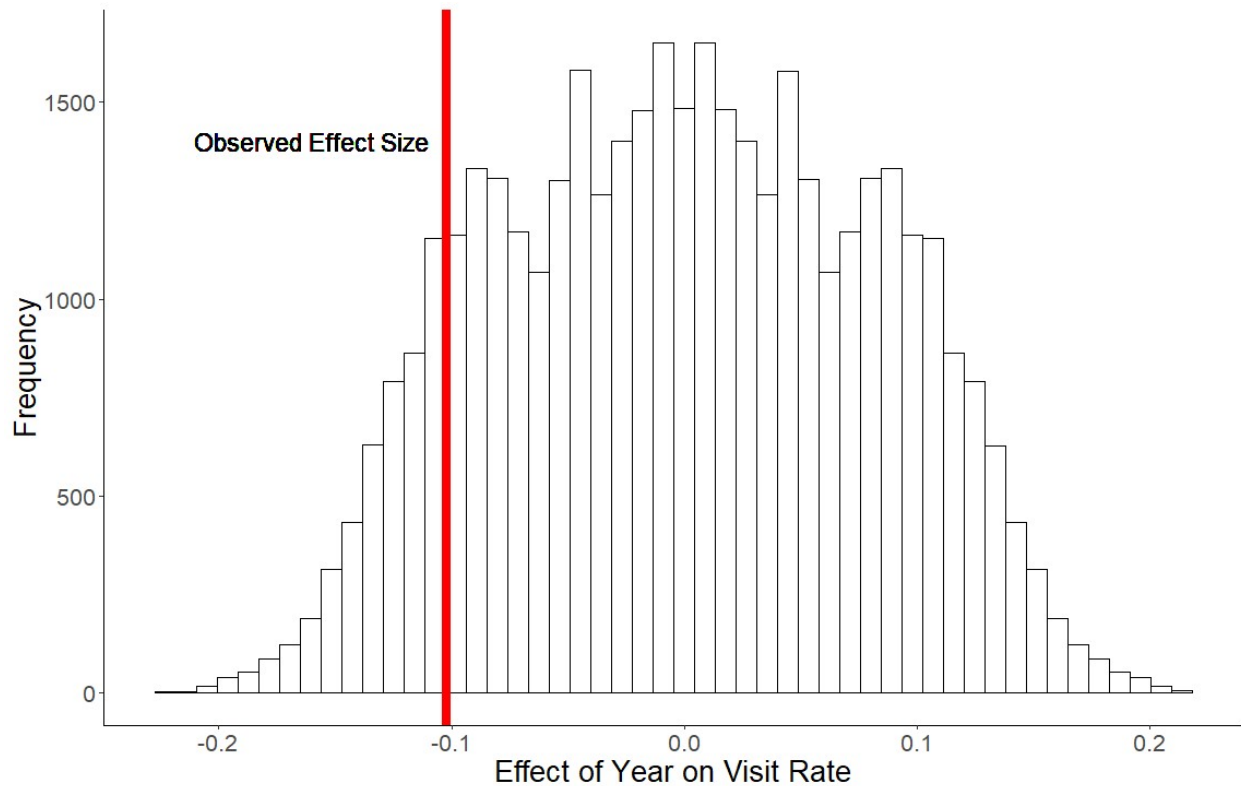
The data provides compelling evidence that the regional rate of visitation, and thus the ecosystem function provided, by wild bees to watermelon flowers was significantly lower in the final years of the study period, with the lowest visitation observed in 2012. However, the data also shows a lot of interannual variation in the rate of visitation. Annual mean visitation rates for wild bees ranged from 0.09 to 0.25 visits per 45 second flower observation, with a standard deviation of 0.06. For example, in wild bees a low average visit rate of .17 visits per flower observation in 2007 was followed by an average visit rate of .245 visits per flower observation in 2008; a 44% increase in a single year. This begs the question: Given the variability in visit rates between years, how likely would we be to find a decline over 7 years just by chance? Over a sufficiently short time series, a measured change in visitation could result from a random draw from a stochastic process with high variability, rather than being indicative of any underlying change in conditions. In order to estimate the likelihood of our observed changes in visitation, given the inter-annual variability encountered, I conducted a permutation analysis on the wild bee data set<sup>1</sup>. Years were reassigned in all 40,320 possible sequences between 2005 and 2012, and negative binomial

<sup>1</sup> Because of the excessively long computational times, the code for permutation analysis will not run automatically in the R script provided with this assignment.



regressions were re-run for each sequence. The reported p-values are equal to the fraction of these permutations that had coefficients as or more extreme than those observed. A small p-value would be indicative of a real decline in the base rate of visitation, more so than might be expected in 8 years of random fluctuations. Our permutation test of the effect of year on visitation by wild pollinators resulted in  $p = 0.118$ . This suggests that given the inter-annual variation encountered in our study, we would expect to find a decline in visit rate as steep or more so only 11.8% of the time purely by chance (Figure 5).





*Figure 5: Results of a permutation analysis on the effect of year. Years were reassigned in all possible combinations, and the model coefficients for the effect of year extracted. This histogram shows the frequency of model coefficient values. The red line represents the model coefficient value for the real data. 11.8% of permuted coefficient values were as or more negative than the observed value. Applied to the wild bee data set (sans *A. mellifera*).*

## Discussion

Despite the paucity of long-term studies monitoring bee abundance, it has been shown that normal inter-annual variation in the size of bee communities, and by proxy the ecosystem services they provide, can be quite large, in natural habitats everywhere from tropical rainforests to Mediterranean scrub [22,23,35]. The rate of visitation at watermelon flowers at farms in New Jersey and Pennsylvania from 2005 to 2012 lends further support to this tenet, though this time from a single-crop perspective in an agricultural environment. A recent meta-study that looked at changes in pollinator abundance in paired years from multiple crop-systems at a global scale also found large interannual variation in pollinator abundance (Senapathi et al., 2021). Furthermore, our analyses highlight the challenges facing those who wish to study long-term trends in bee abundance and pollinator service provision: even with six years of data collection, natural fluctuations in abundance make discerning underlying trends difficult. In our study system overall visitation rates by wild bees declined by over half, but permutation analysis suggests that finding such a large decline in the absence of any underlying downward trend in conditions is not unreasonable likely. To identify long term trends in bee abundances, many more years of data will be needed. While many pollinator species may be in decline across the world[36], the majority of ecosystem services provided in any given place or time are provided by a handful of dominant species [37], making it difficult to infer net changes in ecosystem service provision from landscape-scale changes occupancy, richness or diversity. These are not new realizations by any means; in fact, they were the main conclusions from a National

Center for Ecological Analysis and Synthesis workshop in 1999, which was tasked with evaluating the evidence of, and potential for, catastrophic pollinator declines in North America [38]. David Roubik [35] made the case for a minimum of four years of monitoring to detect trends, based on his work with Euglossine bees, but in light of our results that number may be too conservative for some systems. It's been over 20 years since the NCEAR workshop published its conclusions, and the work they called for hasn't been done. Fortunately, there is now building momentum to fund and conduct long-term monitoring of pollinator populations, including bees [11,12]. Hopefully the coming decades will see more fruitful assessment of trends in bee populations and the services they provide as a result.

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