Sub-lethal concentrations of neonicotinoid insecticides at the field level affect negatively honey yield: Evidence from a 6-year survey of Greek apiaries

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Abstract

The threats posed by neonicotinoid insecticides to bee populations have been the focus of considerable research. Previous work has shed new light on the effects of neonicotinoids on bees by uncovering pathways through which neonicotinoids affect bee population dynamics and the potential interactions they have with exogenous stressors. Yet, little is known about whether these effects translate in a field-relevant setting to substantial losses in honey yields for commercial beekeepers. Here, we used data from a 6-year survey of 60 apiaries in Greece and economic modelling to assess at the field level the effects of neonicotinoid insecticides on honey production. Based on production function estimates, we found that sub-lethal concentrations of two widely used neonicotinoid insecticides (imidacloprid and thiamethoxam) detected in the nectar of flowers resulted in substantial losses in honey production for commercial beekeepers in our sample. By simulating a scenario with ideal pathogenic and environmental conditions, we found that the magnitude of the neonicotinoid effects decreases significantly under ideal conditions providing evidence for possible synergies at the field between neonicotinoids and environmental and pathogenic factors. Moreover, in a replicated study with grouped apiaries, we found evidence that the marginal effects of neonicotinoids on honey production may vary across apiaries facing different conditions.

Introduction

Apiculture is a vital part of the agricultural economy in many developed and developing countries (*1*). According to the FAO, the total number of managed honeybee colonies worldwide was 90.4 million in 2016. Those colonies yielded approximately 1.8 million tonnes of honey production with a gross value of approximately 6.4 billion US dollars (*2*). Thus, any threats to apicultural production could have serious consequences for agricultural economy and the livelihoods of thousands of professional and semi-professional beekeepers worldwide (*1, 3*).

Neonicotinoid insecticides, widely used to manage crop pests, have been widely perceived as a threat to honeybee populations (*4–8*) and therefore for apicultural

production (*9*). Although neonicotinoids are not commonly encountered at lethal doses in the field, recent studies have shown that exposure to sub-lethal concentrations distort bee population dynamics by impairing worker bees' homing ability (*10, 11*), impairing foraging activity (*5, 12*), and reducing colonies' overwinter survival (*13, 14*) and reproductive success (*6, 15*). Neonicotinoids have also been shown to interact with infectious organisms (*7, 16, 17*), food stress (*7*), and local conditions (*14*) to produce negative outcomes for bees.

However, although previous work has significantly advanced our understanding on the effects of neonicotinoids, most of it has focused on the direct effects on bees themselves (*18, 19*) and not on the indirect effects on honey yields. Equally important, most research was conducted in laboratory or semi-field settings that are not representative of production conditions actually faced by commercial beekeepers. Thus, the degree to which neonicotinoids can decrease commercial honey production, either on their own or synergistically with environmental and pathogenic factors, remains largely unstudied and thus unknown. A quantitative assessment of those effects in a field-relevant setting is needed to enhance our knowledge base and to inform appropriate responses by policymakers and the public.

In this paper, we use data from a 6-year field survey of 60 apiaries in Greece and economic modelling to assess the effects of neonicotinoid insecticides on honey production. Our study aims to examine the degree to which field-level concentrations of neonicotinoid insecticides result in reductions in honey production for beekeepers. Our study aims also to investigate possible synergetic interactions of neonicotinoids with environmental and pathogenic conditions in the apiaries and quantify the effects of these synergies on honey yields.

Data and Model Description

We investigated the effects of neonicotinoid insecticides on honey production levels using field data for commercial beekeepers. The data involved 60 randomly selected commercial apiaries located in 10 spatially separated (> 24 km) farming-intensive areas on the island of Crete in Greece (6 apiaries per area).

The apiaries and the surrounding landscapes were inspected at the beginning and the end of the honey season (May and October, respectively) for 6 consecutive years from 2006-2011. In each inspection, samples of flower nectar were taken from multiple spots within a 2 km distance from the apiaries that covers the likely foraging range of honeybees (*20*). The sampling spots were selected based on the number of visits of honeybee foragers at flowers accounting thus for possible preferences of foragers for foods containing neonicotinoid residues (*21*). At the first inspection of each season (May), on-site measurements on honeybee populations were made on 4-18 randomly selected hives per apiary. Adult bee and brood comb samples were also taken from the selected hives to be tested for the presence of common pathogenic honeybee parasites frequently encountered in Greek beekeeping (*22*). At the time of the second inspection (October), information on seasonal honey production volumes and input usage were retrieved directly from beekeepers' accounting books. In addition, semi-structured interviews were conducted with beekeepers about beekeeping and hive relocation practices used (Details on study design and measurement methods used are presented in the Supporting Information section).

Adult bee and brood comb samples were tested in specialized biology laboratories for the presence of common honey bee infectious agents. Molecular and electron microscopy analysis indicated negative and low-positive samples of *Nosema* apis (Cp = 39.4 ± 0.4), *Nosema* ceranae (Cp = 39.1 ± 0.3), CBPV (Cp = 37.4 ± 0.5), DWV (Cp = 38.8 ± 0.2), ABPV (Cp = 39.9 ± 0.1), and SBV (Cp = 39.8 ± 0.1). On the other hand,

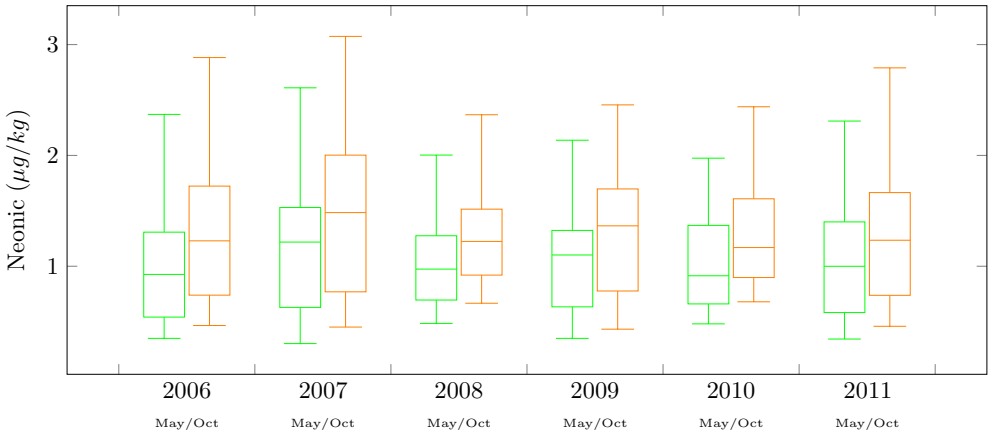

Fig 1. Neonicotinoid concentrations. The box-plots provide information about neonicotinoid concentrations levels in nectar from all areas sampled, pooled according to years and seasons. Green and orange lines refer to spring and autumn seasons, respectively.

97% of the adult bee samples were diagnosed as positive to Varroa destructor (Varroa mite) with a mean Cp=17.68 ± 1.6 (Mean Crossing point value ± s.d.). Therefore, only mite infestation was considered in the analysis as the only infectious pathogen traced at significantly high levels.

The samples of nectar were analyzed in a general chemical state laboratory (Laboratory of Analytical Chemistry of the University of Crete) for the presence of 5 neonicotinoid compounds: imidacloprid, thiamethoxam, clothianidin, acetamiprid and thiacloprid; and a pyrethroid: Λ-cyhalotrin. All samples were negative to clothianidin and Λ-cyhalotrin. Hence, four systemic compounds of neonicotinoids (imidacloprid, thiamethoxam, acetamiprid and thiacloprid) were detected in the samples. Acetamiprid and thiacloprid were traced at very low proportions (< 1%) and therefore were not considered in the analysis. Besides being traced at insignificant levels, these two compounds have been shown to result in lower acute toxicity for bees compared to imidacloprid and thiamethoxam (*23, 24*). Excluding them should have a minor quantitative influence on the study findings.

Imidacloprid and thiamethoxam elicit similar toxicity effects per concentration unit (*24*) which allows their direct aggregation to construct an additive measure of neonicotinoid concentration. The two compounds were detected together in concentrations between 0.377 $\mu g/kg$ and 2.842 $\mu g/kg$ with a mean value of 1.386 ± 0.6 $\mu g/kg$ (mean ± s.d.). These values are well below the documented lethal-dose levels (LD50 <) but high enough to be suspected for sub-lethal effects (*17*). Analyzing the temporal variation and range of the neonicotinoid levels, our data provided evidence for increased accumulation of neonicotinoids in the natural habitat of honeybees between May (1.241 ± 0.5 $\mu g/kg$) and October (1.530 ± 0.6 $\mu g/kg$) implying possible chronic exposure leading to delayed effects over the honey season (*25*). This result can be also attributed to a more intensive use of neonicotinoid insecticides by farmers later in the season. Nevertheless, there was no indication about the persistence of neonicotinoids in the environment over winter periods (Figure 1). The later result could be attributed to decreases in insecticide use intensity during the winter seasons and to intense rainfalls commonly occurring in winter months which may washed neonicotinoid residues out of honeybees' habitats.

To assess the effects of neonicotinoids on honey production, we followed a two-step modelling strategy. First, using the concept of a damage function borrowed from the extensive damage and control literature (*26–28*), we modeled the effects of neonicotinoids on the biological process of honeybees. Second, bee density composed of the initial bee

Table 1. Honeybees and honey production: Damage measures at actual neonicotinoid levels and estimated responses to potential changes in neonicotinoid levels. The 60 apiaries in the samples were sorted with an increasing order based on the neonicotinoid concentrations observed in the surrounding areas. Next, they were grouped into five equal neonicotinoid quantiles with the first quantile including the 12 apiaries exposed to the lowest neonicotinoid levels, the second quantile including the 12 apiaries exposed to higher neonicotinoid levels and so on. Annual average values are shown per neonicotinoid quantile.

	Neonicotinoid Quantiles					Mean
	1st	2nd	3rd	4th	5th	Values
Managed Honeybee Population						
Estimated Losses						
Percentage Losses (in %)	9.44	19.54	24.36	18.43	20.06	18.37
Absolute Losses (in 000's of bees)	636.4	1,142.2	1,351.7	1,159.0	840.8	1,026.0
Estimated Responses to Changes in Neonics Levels						
Percentage Response to +1% (in %)	0.100	0.221	0.281	0.208	0.233	0.208
Absolute Response to +0.05 $\mu g/kg$ (in 000's of bees)	75.2	67.6	63.2	44.8	23.1	54.8
Absolute Response to +0.10 $\mu g/kg$ (in 000's of bees)	149.2	134.0	125.5	89.2	46.0	108.8
Honey Production						
Estimated Losses						
Percentage Losses (in %)	2.51	6.55	8.64	6.71	9.50	6.78
Absolute Losses (in *kgs* of honey)	218.5	437.4	602.4	458.1	526.0	448.5
Estimated Responses to Changes in Neonics Levels						
Percentage Response to +1% (in %)	0.029	0.087	0.118	0.087	0.125	0.089
Absolute Response to +0.05 $\mu g/kg$ (in *kgs* of honey)	38.8	35.1	31.0	24.5	19.2	29.7
Absolute Response to +0.10 $\mu g/kg$ (in *kgs* of honey)	78.2	70.8	62.6	49.3	38.4	59.9
Area and Apiary Characteristics						
Neonicotinoid Concentration (in $\mu g/kg$)	0.659	1.088	1.325	1.672	2.184	1.386
Apiary Size (in 000's of bees)	6,291.7	5,570.0	5,396.1	5,702.2	3,650.0	5,322.0
Aridity Index	0.874	0.537	0.518	1.094	0.947	0.794
Relative Humidity (in %)	0.440	0.491	0.508	0.409	0.354	0.441
Winter Precipitation (in *mm*)	381.3	401.9	368.1	429.4	529.6	422.1
Mite Infestation (in 000's of Mites)	5.73	5.62	5.00	5.50	5.68	5.51

population and the damage function was incorporated into an economic honey-production model. Using the sample data, the model was parametrically estimated in one stage (Details on the proposed model are presented in the Supporting Information section).

Neonicotinoids have been shown to act both in isolation and in synergy with other factors (*5, 11–12, 14*). Thus, both neonicotinoids alone and their interactions with mite infestation, food resources, and weather conditions were included in the damage function. However, the own terms of the later set of factors (mite infestation, food resources, and weather conditions) was not included into the specification of the damage function due to important multicollinearity issues. The consequence is that our results may reflect a higher-bound estimate of the interactive effects of neonicotinoids on honeybee population and honey production since the corresponding interaction terms may absorb also part of the direct effects of these factors. In addition, other factors including bee genetics, removing strategy of livestock (*1*), and beekeeper's education (*29*) are known to influence colony losses and therefore should be included into the damage function. However, these factors present zero or little variation across beekeepers in our sample and thus could not be considered in our regression analysis. Other insecticides and pollutants are also known to influence alone or synergetically with neonicotinoids the honeybee populations (*30–31*). However, there was no indication that other insecticides (other than those analyzed) were present in the surveyed areas, at least at significant levels (More information about the choice of the compounds analyzed is presented in the Supporting Information section).

Results and Discussion

Our results indicated an average loss of 18.37 ± 8.5% in managed honeybee populations due to neonicotinoid effects (Table 1, upper panel) which is in line with previous findings (*3, 7*). That corresponds to annual losses of 1.02 ± 0.6 million honeybees for an average-

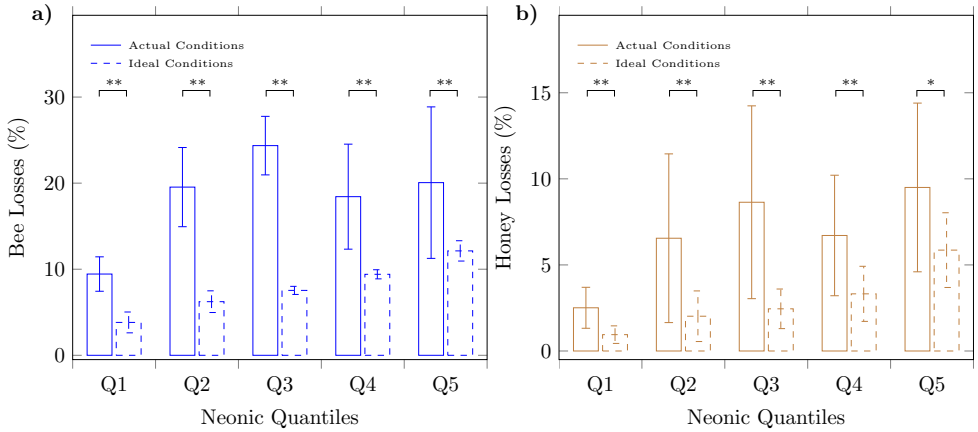

Fig 2. Honeybee and honey losses per neonicotinoid quantile under actual and under ideal conditions. a, b, Mean losses in managed honeybee population (**a**) and honey production (**b**) under actual and ideal field conditions. Details about the construction of neonicotinoid quantiles are provided in the caption of Table 1. Solid and stippled lines refer to actual and ideal conditions, respectively. Means ± s.d. are shown separately for every neonicotinoid quantile. Results from one-tailed paired t-test are shown; $^{**}p < 0.01$,$^{*}p < 0.05$.

sized apiary in our sample (average apiary: 133 hives, 5.32 million honeybees). Our results indicated average losses in honey production of 6.78 ± 4.7% which translates into losses of 448.5 ± 31.6 kg of honey per season for an average-sized apiary (Table 1, middle panel). For the whole six year period, honey losses were estimated at 161.5 tonnes for the 60 apiaries analyzed.

To determine the responsiveness of honey production to incremental changes in neonicotinoid concentrations, we performed a marginal analysis based on the parameter estimates of the model. We found that, other things equal, a 1 per cent increase in the neonicotinoid concentrations results in losses of 0.208 ± 0.11% and 0.089 ± 0.05% in honeybee population and honey production, respectively. We repeated the marginal analysis in absolute terms assuming incremental increases of 0.05 and 0.10 $\mu g/kg$ in neonicotinoid levels. We found the corresponding losses in honey production to be 29.7 ± 15 kg and 59.9 ± 31 kg per season for an average-sized apiary (Table 1, middle panel).

The effects of neonicotinoids on honey production are expected to increase at higher concentrations. But precisely how these effects vary with concentration levels cannot be determined *ex ante*. Therefore, we used our estimated model to identify empirically how honey production responds to increasing the concentration of neonicotinoids. Sample apiaries were sorted by exposure levels detected in the surrounding areas and then grouped into equal neonicotinoid quantiles. The first quantile included the 12 apiaries exposed to the lowest neonicotinoid concentrations, the second quantile included the 12 apiaries exposed to higher concentration levels, and so on.

We found that losses in honey production are correlated to losses in honeybee population in the same quantiles but not with apiary size. We also found that apiaries in the first quantile, which were exposed on average to 0.659 $\mu g/kg$ of imidacloprid and thiamethoxam, experienced significantly lower losses in honeybee population and honey production when compared with apiaries in higher quantiles (Table 1). We did not, however, observe significant increasing losses across the remaining four higher neonicotinoid quantiles. These insignificant linear trends might be attributed to differences in environmental and pathogenic conditions across apiaries which may have altered the magnitude of the neonicotinoid effects on honeybee population and honey production. It

should be mentioned though that the trends are generally consistent and vary according to residue levels, which is indicative of a cause-effect relationship.

To examine whether our results were sensitive to differences in environmental and pathogenic conditions in the field (Table 1, lower panel), we simulated a scenario in which all sample apiaries are facing equal field conditions. We did so by assigning a predetermined set of fixed values to the condition-related variables of the model. The set of values was determined so as to reflect near-ideal conditions in the apiaries (Ideal conditions: winter precipitation=$520mm$ of rain as a proxy of food resources, aridity index=0.83 and relative humidity=58% as proxies of weather conditions, number of mites=0). Then, we used the estimated model to project responses of honey production to increases in neonicotinoid levels. We found that under ideal conditions, honey losses increase robustly across all neonicotinoid quantiles (Figure 2). We also found honey losses to be considerably smaller compared to those under actual conditions in all five neonicotinoid quantiles (one-tailed paired t-test: $t > 2.17$, $df = 11$, $p < 0.026$) providing evidence that the magnitude of neonicotinoid effects depends upon environmental and pathogenic conditions. This finding suggests a possible presence of synergies at the field between neonicotinoids and environmental and pathogenic conditions.

To investigate the extent to which adverse conditions may have increased the magnitude of the neonicotinoid effects, we classified apiaries into two equal groups based on environmental and pathogenic conditions and then replicated the simulation analysis for each group. The first group included the apiaries facing the least adverse conditions and the second group included those facing the most adverse conditions. Under ideal conditions, we found quite similar neonicotinoid effects across the two groups. Under actual conditions, we found significantly higher effects for the second group facing the most adverse conditions (Figure 3). In both groups, neonicotinoid effects were found to increase in general with increasing concentrations. However, the severity of these effects across concentration levels was different between the two groups. Honey losses followed a logarithmic trend with concentration levels in the first group and an exponential trend in the second group implying decreasing and increasing marginal effects, respectively.

To obtain a quantitative assessment of the interactive effects of neonicontoinoids, we conducted a variance analysis within each group considering the mean difference between the honey losses under actual conditions and the honey losses that would have occurred under ideal conditions. Our results indicated that deviations from ideal conditions increased honey losses by 2.53% $\pm$ 2.03 for apiaries facing the least adverse conditions and by 5.28% $\pm$ 4.60 for apiaries facing the most adverse conditions. Focusing on concentrations higher than 1.5 $\mu g/kg$, we found that the increase in honey losses due to interactive effects were 2.76% $\pm$ 2.16 for apiaries facing the least adverse conditions and 8.63% $\pm$ 6.40 for apiaries facing the most adverse conditions.

Conclusion

In this paper, we used data from a 6-year survey of 60 apiaries in Greece and economic modelling to assess the effects of neonicotinoid insecticides on honey production. Our results indicated that sub-lethal concentrations of neonicotinoids detected in the nectar of flowers resulted in substantial losses in honey production levels for beekeepers in our sample. This finding is important because it improves our understanding of the economic welfare losses associated with neonicotinoid exposure. Our results provided also evidence for possible synergisms at the field between neonicotinoids and environmental and pathogenic conditions prevailing at the apiaries. These synergetic effects were found to account for significant losses in the honey yields of beekeepers. However, estimated losses reflect only a higher bound estimate of the interactive effects of neonicotinoids. Finally, our results indicated decreasing marginal effects of neonicotinoids on honey

production for beekeepers in our sample facing the least adverse conditions and increasing marginal effects for beekeepers facing the most adverse conditions. This result indicates that potential increases in neonicotinoid levels are likely to lead to higher losses in honey production under adverse conditions, especially if neonicotinoids are already present at high concentrations.

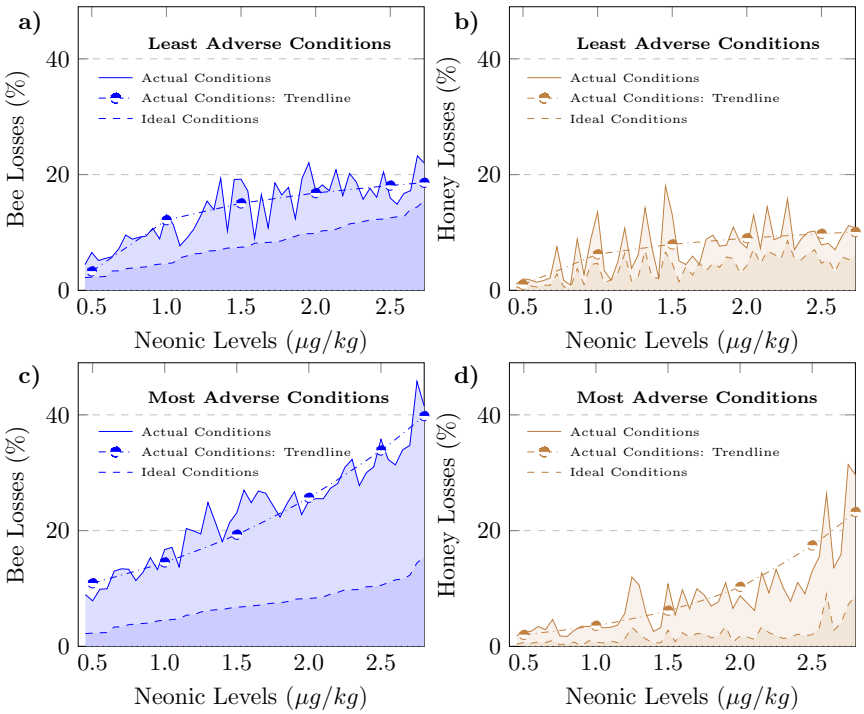

Fig 3. Honeybee and honey losses across neonicotinoid concentrations for the groups of apiaries facing the least and most adverse conditions. a- d, Mean losses in managed honeybee population under actual and ideal conditions for apiaries facing the least adverse conditions (**a**), mean losses in honey production under actual and ideal conditions for apiaries facing the least adverse conditions (**b**), mean losses in managed honeybee population under actual and ideal conditions for apiaries facing the most adverse conditions (**c**), mean losses in honey production under actual and ideal conditions for apiaries facing the most adverse conditions (**d**). Based on the parameter estimates of the damage function and actual data on weather conditions and mite infestation, an index of the overall conditions prevailing at the apiaries every season was constructed. Based on the index, apiaries were classified into two equal groups with the first and second group including the apiaries facing the least and most adverse conditions, respectively. The choice of functional form for the trend lines was based on goodness-of-fit measures. Three alternative functional forms were considered for the approximation of the trend lines, namely, the linear, logarithmic and exponential functional form.

Table S1. Summary Statistics of the Variables

Variable	Mean	Min	Max	Std.Dev.
Output and Inputs				
Honey Production (in kgs)	3,160	802	8,508	1,671
Veterinary Expenses (in Euros)	242	74	787	135
Intermediate Inputs (in Euros)	1,867	488	10,761	1,680
Family Labor (in hours)	322	62	1,167	170
Capital Stock (in Euros)	3,076	333	14,507	2,639
Number of Bees (in 000s)	5,324	1,880	14,000	2,522
Bee Farm Characteristics				
Mite Infestation (No of Mites)	5,507	1,872	13,051	1,864
Winter Precipitation (in mm)	422	1,072	216	147
Relative Humidity (%)	0.44	0.24	0.61	0.086
Aridity Index	0.79	0.35	1.49	0.33
Damaging Input				
Neonicotinoids (in $\mu g/kg$)	1.386	0.377	2.842	0.614

Supporting information

Model setup

A two-step approach was adopted for modelling the effects of neonicotinoids on honey production. In the first step, neonicotinoids, neonicotinoids × mite infestation, neonicotinoids × winter precipitation, neonicotinoids × humidity, and neonicotinoids × aridity were embedded into a damage function defined in generic form as (*26–28*) $\phi_{it}\left(z_{it}, \boldsymbol{s_{it}}; \boldsymbol{\alpha}\right)$, where i indexes the apiaries, t indicates the time period, $\phi : \Re_{+}^{5} \rightarrow [0, 1]$ is the damage function having the properties of a cumulative probability distribution, $z \in \Re$ denotes neonicotinoid concentration, $s \in \Re_{+}^{4}$ is the vector of exogenous variables including mite infestation levels proxied by the number of mites per hive, food resource availability proxied by winter precipitation, and weather conditions proxied by relative humidity and the aridity index and α's are parameters to be estimated. Bee density, $\tilde{b}$, was defined in each apiary as:

$$\tilde{b}_{it} = b_{it}\left[1 - \phi_{it}\right] \tag{1}$$

where b_{it} is bee population at the beginning of the honey season. In the second step, bee density was embodied within a honey production function defined as: $y_{it} = f\left(\tilde{b}_{it}, \boldsymbol{x_{it}}, t; \boldsymbol{\beta}\right)$, where $y \in \Re$ is output, $f : \Re_{+}^{j+2} \rightarrow \Re_{+}$, is a continuous and, strictly increasing, twice differentiable concave production function, representing maximal output from honeybee density and productive inputs given the exogenous variables and the available technology, $x \in \Re_{+}^{4}$ is a vector of productive inputs including veterinary expenses, intermediate inputs, family labor, and capital stock, and β's are parameters to be estimated. Summary statistics of the variables are presented in Table S1.

Functional forms

The following exponential functional specification embodying the biological relationships involved in the growth and development of honeybee populations was used to approximate the damage function (*27*):

$$\phi_{it} = 1 - exp\left(-\alpha_z z_{it} - \sum_{q} a_{zq} z_{it} s_{qit}\right) \tag{2}$$

Table S2. Parameter Estimates of the Translog Production Function

Par.	Est.	St. Error	Par.	Est.	St. Error
β_0	0.8572	0.0262**	β_{VV}	0.2970	0.1329**
β_B	0.3059	0.0853**	β_{IL}	-0.1344	0.1053
β_I	0.1661	0.0269**	β_{IC}	-0.0513	0.0693
β_L	0.1701	0.0402**	β_{IV}	0.2521	0.1374*
β_C	0.1080	0.0252**	β_{LC}	0.0112	0.1127
β_V	0.1837	0.0416**	β_{LV}	-0.4706	0.2226**
β_T	0.0698	0.0314**	β_{CV}	-0.3932	0.1208**
β_{TT}	0.1309	0.0606**	β_{BI}	-0.4476	0.1644**
β_{BT}	0.0066	0.0711	β_{BL}	0.9004	0.1975**
β_{IT}	0.0140	0.0321	β_{BC}	0.3735	0.1135**
β_{LT}	-0.0336	0.0424	β_{BV}	0.0977	0.2275
β_{CT}	0.0158	0.0237	α_Z	-0.4988	0.1512**
β_{VT}	0.0143	0.0535	α_{ZM}	-0.0875	0.0504*
β_{BB}	-0.6035	0.2434**	α_{ZP}	0.2468	0.0653**
β_{II}	-0.0261	0.0758	α_{ZH}	-0.0262	0.0817
β_{LL}	0.0372	0.0786	α_{ZA}	0.1402	0.0457**
β_{CC}	0.0426	0.0315	$\bar{R}^2$	0.8848	

B refers to bee density, I to intermediate inputs, L to family labor, C to capital, V to veterinary expenses, T to time, Z to insecticides, M to mite infestation, P to winter precipitation, H to relative humidity, and A to aridity index,. Robust standard errors are reported in the table. * and ** indicate statistical significance at the 10 and 5 per cent level, respectively.

For the approximation of the production function, we used the following flexible transcendental logarithmic (translog) functional specification (*33*):

$$\begin{aligned}\ln y_{it} = {} & \beta_0 + \beta_b \ln \tilde{b}_{it} + \sum_j \beta_j \ln x_{jit} \\ & + t\left[\beta_t + \frac{1}{2}\beta_{tt} t + \beta_{bt} \ln \tilde{b}_{it} + \sum_j \beta_{jt} \ln x_{jit}\right] \\ & + \frac{1}{2}\left[\beta_{bb} \ln^2 \tilde{b}_{it} + \sum_j \sum_\rho \beta_{j\rho} \ln x_{jit} \ln x_{\rho it}\right. \\ & \left. + \sum_j \beta_{bj} \ln \tilde{b}_{it} \ln x_{jit}\right] + v_{it} \end{aligned} \quad (3)$$

where $v_{it} \sim N\left(0, \sigma_v^2\right)$ is a normally distributed error term capturing omitted explanatory variables and measurement errors in the variables. Upon substituting (2) into (1) and then into (3), the resulting model was estimated in one stage providing estimates for α and β parameters. Parameter estimates of the model are reported in Table S2.

Measurement of neonicotinoid effects

Measurements on the percentage losses in honeybee populations were obtained directly by the fitted values of the damage function ($\hat{\phi}_{it}$). The number of bees lost (absolute losses) was computed as $b_{it} \times \hat{\phi}_{it}$. Honey losses in each apiary were measured as the maximal possible honey production that would have been realized in the absence of neonicotinoids minus the maximal possible honey production in the presence of neonicotinoids at their

actual levels. The later was obtained by the fitted values of the production function and the former by the fitted values of the production function after imposing z=0 in relation (2). To project losses in bee population and honey production under ideal conditions, we assigned a set of fixed values to the condition-related variables included in vector $s \in \Re_+^4$ and then repeated the measurements as described above. The set of fixed values was determined so as to reflect near-ideal conditions in the apiaries.

Survey design

The survey included 60 randomly selected apiaries owned by professional beekeepers located in ten spatially separated areas (>24km) in the Western part of the island of Crete in Greece. An equal number of apiaries was selected from each area resulting in 6 apiaries per area. The 10 areas were selected randomly from a total of 38 areas in the western part of the island where professional beekeepers are known to maintain their apiaries. A pilot survey was conducted in August 2005. In the course of the pilot survey, the areas surrounding the apiaries were inspected and information on the spatial characteristics, geographical proximity and floral diversity of the areas were recorded. Areas' inspection revealed areas that were very homogeneous over these characteristics and closely located apiaries typically adjacent to each other. During the pilot survey, all apiary owners were interviewed and agreed to participate in the survey. Preliminary interview results indicated that beekeepers were using similar relocation practices including three moves during the year in the middle of October (to overwinter), beginning of March (to restore colonies' strength) and beginning of May (for the honey harvesting period). Hence, beekeepers were highly homogenous with respect to the relocation practices used indicating that this variable is constant in our sample. Preliminary interview results indicated also that the first exposure of honeybees to neonicotinoids during the year was in the beginning of the honey season when they were relocated to the apiary sites. Before this move, all beekeepers indicated that they maintained the hives in non farming areas (from October to April). In addition, interview results indicated that beekeepers commonly perform hive splitting tasks shortly before the relocation of hives to the apiary sites for the honey season. All apiary owners agreed to inform in advance the survey team about the hive relocation dates. Finally, in the course of the pilot survey, 10-15 crop farm operators from each area within a distance of 5km from the apiaries were interviewed about the types of insecticides used. Based on this information, the compounds of neonicotinoids which were likely to be present in the surrounding areas were identified. The main survey commenced in 2006 and took place for 6 consecutive years until 2011 that is shortly before EU imposed a moratorium in the use of neonicotinoid insecticides (*34*). In the course of the survey, all 60 apiaries in the sample were inspected twice per year at the beginning (28 Apr - 15 May) and the end (28 Sep - 15 Oct) of the honey season, respectively. In the course of the first inspection of each season, area-specific measurements on neonicotinoid concentrations were performed. Moreover, at each apiary, measurements on honeybee populations were performed and brood comb samples were collected from hives. In the course of the second inspection of each season, area-specific measurements on neonicotinoid concentrations were repeated. Moreover, beekeepers' accounting books were reviewed and personal interviews were performed with apiary owners. In addition, four visits were made to all apiaries in the middle of the seasons at the beginning of months June, July, August and September and measurements were performed on mite infestation levels. The survey was partly supported by the Specific Targeted Research Sixth Framework EU Project TEAMPEST under contract number 212120 and was conducted in cooperation with National Agricultural Research Foundation (NAGREF).

Nectar samples

Nectar samples from flowers and herbaceous plants were collected twice per year between 1 May and 15 May and between 28 Sep and 12 Oct. In each area, 12 nectar samples were taken in the course of each inspection from different spots within a $2km$ distance from the apiaries (*20*). This distance corresponds to two times the average honeybee foraging range, $1km$ (*35*). Hence, contaminated resources located farther away from the average honeybee foraging range have been also taken into account. The sampling spots were selected based on the number of visits of honeybee foragers at flowers. Specifically, nectar foraging in each area was observed for two hours per day within a period of 5 days. Observation periods were from 9:00-10:00 and from 16:30-17:30. Observations were made by 12 observers, each assigned to monitor fields of about 1 km^2. During the first day, the landscape within each field was inspected by the corresponding observer and all floral grasslands were marked with cable ties. In the following two days, the marked grasslands were observed and the most visited grassland within each field of responsibility was identified for subsequent observation. The most visited grassland was divided into sub-fields of $40m^2$. During the following two days, the sub-field exhibiting the highest visitability was identified and tagged for further observation. All flowers within the sub-field were marked with numbers. In the course of the fourth and fifth day, the number of honeybee visits at each flower was recorded within the tagged sub-field. Observers considered as visits only those lasted more than 5 seconds. The average time spent by honeybees per visit was measured at $8.1\pm$ 1.4 seconds with very little variation across areas. Nectar samples were next collected from the most visited plant in each sub-field resulting in 12 samples from each area. No process was used to validate that honeybees observed were from the surveyed apiaries. However, this is not expected to introduce important bias in the measurements since the visits were used as an instrument to select the sampling spots. Alternatively, sampling spots could have been randomly selected. At least, 1.5 grams of nectar were collected per sample in the course of each inspection indicating a minimum of 18 grams of nectar from every area. To examine if the selection of different spots would result in different measurements in neonicotinoid concentrations, we performed a set of post hoc distributional tests on concentrations detected in area-specific multiple spot samples. Statistical testing results using the Kolmogorov-Smirnov test failed to reject the hypothesis of a uniform distribution of neonicotinoids across each inspected area ($D < 0.25$, $n = 12$, $\alpha = 0.05$) suggesting possibly equally contaminated fields. This result indicates that selecting different sampling spots within each area would not be likely to make any statistically significant difference in the measurement of neonicotinoid concentrations.

Neonicotinoid concentrations

Nectar samples were analyzed in the Laboratory of Analytical Chemistry of the University of Crete (Division of Environment and Analytical Chemistry, Department of Chemistry, University of Crete, Heraklion City, Island of Crete, Greece). Nectar samples were analyzed for the presence of 5 neonicotinoid compounds: imidacloprid, thiamethoxam, clothianidin, acetamiprid and thiacloprid; and a pyrethroid: Λ-cyhalotrin. Concentrations were quantified using liquid chromatography with tandem mass spectrometry (*35*). Neonicotinoid levels detected in the 12 samples from each area were averaged to define the mean concentration of the area (Limits of detection: 0.1-10$\mu g/kg$). Since the measurements were referring to two points of time within each season (beginning and end of the honey season), the two means were also averaged and the resulting figure was used to determine neonicotinoid levels within each area and for each season. The distance of the sampling spot from the apiaries was not considered when calculating the mean concentration of neonicotinoids in each area. This is because concentrations detected

in each area were found to follow a uniform distribution. Therefore, down-weighting concentration levels by distance would not make any difference in the measurements.

Adult bee and brood comb samples

Adult bee and brood comb samples were collected from inside the hives within a period of 3 days from 08 May to 15 May. Between 4 and 18 samples were collected from different hives within each apiary depending on the size of the apiary. This corresponds to the 5-10% of the total number of hives in each apiary. The selection of hives was blinded and was repeated in each season. Therefore, different hives were likely to be considered every season. In addition, adult bee and brood comb samples were collected in the middle of the season within a period of 2 days between 15 July and 30 July to identify possible changes in pathogenic conditions in the apiaries. This sampling process was of a smaller scale involving 1 to 4 hives in each apiary. All samples were tested in specialized biology laboratories for the presence of Nosema apis, Nosema ceranae, Chronic bee paralysis virus (CBPV), Acute paralysis virus (ABPV), Deformed wing virus (DWV), and Sacbrood virus (SBV) using one-step real time RT-PCR for viruses detection and RFLP-PCR for Nosema speciation (*22*). Scanning electron microscopy was also performed on samples for detection of honeybee mites. LightCycler software was used to analyze acquired fluorescence data and the crossing point (Cp), was determined automatically based on the Fit Points method. Samples exhibiting a crossing point (Cp) lower then 35 were defined as positive. Samples exhibiting a Cp between 35 and 40 were defined as low positive while those exhibiting a Cp equal to 40 were defined as negative. The Cp value is the cycle at which fluorescence achieves a defined threshold and corresponds to the cycle at which a statistically significant increase in fluorescence is first detected. Specifically, a threshold line was defined above the noninformative fluorescent data. Next, data points from the log-linear region of the fluorescent curves were used to generate the "best-fit" regression line, namely, crossing line. The intersection of the fluorescent curve with the crossing line was used to determine the fractional cycle number of the crossing point.

Honeybee population

Bee population was measured by visual estimation of adult workers density on comb sides (*37,38*). At each apiary, 4 to18 hives were blindly selected for observation. The exact number of hives was determined by the size of the apiary ensuring that at least the 5% of the hives in each apiary were observed. Selected hives were opened and the combs were sequentially removed. Next, observers visually estimated the percentage of the comb surface covered by adult workers using a pre-marked grid. All visual observations were initiated at 06:30 and completed at 07:15. In cases that the time window was not sufficient to complete all observations in an apiary, the task was continued the following day. All observations were made between 01 May and 19 May. The exact date of observation depended on the relocation date of the hives to the area. Specifically, all observations were made at least one day and at most three days after hives relocated to the apiary sites for the honey season to allow honeybees sufficient time to recover from moving stress (*39*) and minimize exposure time to neonicotinoids since both could potentially affect the measurements. The observed density on comb sides was used to extrapolate the number of bees in each hive (*37*). The estimated populations in each hive were averaged to determine a point estimate of the mean population in each hive. This figure was multiplied by the number of hives in the apiary to proxy the total number of honeybees per apiary. Confidence intervals were build using t-distribution statistical values.

Honey production

Information regarding honey production levels and input usage was retrieved directly from beekeepers accounting books. Accounting books were reviewed in the presence of apiary owners within a period of 2 days between 01 Oct and 12 Oct. Honey production level was determined as the total volume of honey harvested within the season and was measured in kgs. The quantity of honey left in the hives for the needs of honeybees after each harvest was not considered in our analysis due to practical reasons associated with measurement difficulties. The quantity of honey left in the hives was typically predetermined and practices used with respect to this procedure were quite similar across all beekeepers, therefore this exclusion was not expected to have any significant effect on the results. The productive inputs considered in the analysis were intermediate inputs, veterinary expenses, labor input, and capital stock. Intermediate inputs consisted of goods and materials used during the season. These included fuel, electric power, storage expenses, and feeding expenses. The different categories were aggregated into a single input index using the *Tornqvist* approximation to the Divisia index. In particular, national price indices for fuel, electric power, storage and honeybee feed were used to construct an aggregate price for intermediate inputs using the Tornqvist price index (*40*). The cost shares of each type of expenses to total expenses were used as weights in the construction of the aggregate price index. Next, the total cost associated with intermediate inputs was divided by the aggregate price index. The resulting figure was used to measure intermediate inputs. Veterinary expenses, also measured in Euros, consisted of expenses on antibiotics and other medication including miticides and expenses on veterinary physicians. Again, the *Tornqvist* approximation was used to aggregate the above categories. Family labor, measured in working hours, included total family hours (bee farm owner and family members) devoted to working tasks associated with beekeeping. Capital stock measured in Euros included the value of hive boxes and hive frames, smokers and other hive tools, clothing equipment and storing cans. The computation of the capital stock was based on the perpetual inventory method assuming a depreciation rate of 8%.

Mite infestation

Mite infestation at each apiary was proxied by the total number of varroa mites per hive. Four measurements on mite infestation took place during each season between 1-5 June, 1-5 July, 1-7 August, and 1-5 September. At each apiary, 4 to18 hives were blindly selected to be used for measuring mite infestation. The number of mites was estimated using the "sticky board" test method (*41*). Specifically, a sticky board was placed on the bottom of the hive for 48 hours. The number of dead mites falling to the bottom of the hive was next counted. Based on the number of mites found on the sticky board and the mortality rate of mites, their total number was extrapolated. In cases that acaricides had been used by beekeepers to deal with mites, the efficiency rate of the miticide was also accounted for by extrapolating the total number of mites in hive (*41,42*). The estimated number of mites in each hive were averaged to determine a point estimate of the mean number of mites per hive. Since the measurements were referring to four different points of time within each season, the four means were also averaged and the resulting figure was used to determine mite infestation levels within each apiary and for each season. Confidence intervals were built using t-distribution statistical values.

Food resources

Because areas analyzed were homogenous in terms of altitude, soil conditions, and flora diversity, food resource availability was proxied solely by winter precipitation as the

most important factor accounting for differences in flowering time and nectar richness of wildflowers and herbs (*43*). The index was constructed over the period from October to April and it was measured in millimeters of rain. Measurements of the winter precipitation were obtained from the meteorological stations located throughout the island producing continuous spatial grids of weekly air temperature and precipitation. Up to a certain threshold, increases in winter precipitation levels contribute positively to soil fertility (*44*) and flowering time (*43,45*) of plants leading to rich floral resources for honeybees during the honey season. However, because extreme winter precipitation might have the opposite effect, we initially fitted a quadratic term into the model with respect to winter precipitation variable to test for possible non-linear effects. The associated second order parameter was found statistically insignificant implying that winter precipitation was not exhibiting a certain threshold. Thus, the quadratic term was not considered in the final model.

Weather conditions

Weather conditions in each area were proxied by relative humidity and aridity levels since both weather variables can interact significantly with neonicotinoids influencing the foraging activity of bees. The aridity index was constructed as the ratio of the average ambient temperature over the total precipitation in the area where apiaries were located (*46*). Both relative humidity and aridity index were computed over the period from 1 May to 12 October. The meteorological data for the weather variables were obtained by the local Meteorological Stations located throughout the island. High rates of relative humidity make heavier the wings of honeybees which in turn implies that honeybees need to consume more energy for their flights. As a result, the frequency and duration of the flights are decreased when relative humidity exceeds a certain threshold. In addition, high rates of relative humidity act negatively in the concentration of sugars in the nectar of flowers which in turn reduces the attractiveness of food resources for bees. With food resources being less attractive, honeybees reduce their flights (*47,48*). In overall, high rates of relative humidity rates above a certain threshold are expected to affect negatively the flight activity of honeybees. On the contrary, low rates of relative humidity have no direct effects on the flight activity of Apis species but can increase the attractiveness of resources. Ambient temperature and summer precipitation are both related with the duration and frequency of foragers' flights. Up to a certain threshold, increases in ambient temperature decrease the time and energy required by honeybees to elevate their thoracic temperature before flight contributing thus positively to the foraging activity of bees (*49*). Similarly, low summer precipitation levels increase the frequency of foragers' flights. Therefore, increases in aridity levels up to a certain threshold are expected to enhance foraging. However, extreme temperatures and very low summer precipitation levels might have the opposite effect on flight duration by increasing rapidly the body heat of bees during flight and reducing the attractiveness of flowers. Hence, increases in aridity levels above a certain threshold are expected to contribute negatively to flight duration. To test for such non-linear effects, we added two quadratic terms into our model with respect to relative humidity and aridity variables. However, the associated second order parameters were found statistically insignificant implying that weather conditions were not exhibiting a certain threshold. Thus, the quadratic terms were not considered in the final model.

Ideal Conditions

Ideal conditions were determined within the topographic and vegetation characteristics of the areas where apiaries are located. The study areas are characterized by a semi-arid ecosystem with mediterranean climate, sandy soils, and rich grass- and shrub-lands.

Within this mediterranean-type ecosystem, winter precipitation levels of 450mm to 650mm of rain have been shown to optimize the cation exchange capacity of soil and the phenology of flowers leading to high levels of soil fertility and nectar-rich wildflower grasslands during the honey season (*43,44,50*). Hence, winter precipitation was ideally set within this interval to 520 millimeters of rain (*44*). Flight activity of honeybees has been shown to reach its peak at ambient temperatures between 21 and 26 degrees centigrade with low precipitation levels in the form of light drizzly rains (*51*). Therefore, ambient temperature and summer precipitation were ideally set within these intervals to 23.3 degrees centigrade (*47*), and 28mm of rain resulting in an aridity index of 0.83. At this temperature, relative humidity was ideally set to 58% (*47*). The ideal levels for the aridity index above refer to Apis Cerana and not to Apis Mellifera honeybee. The two species are known to have slightly different ecological requirements. Hence, these values constitute an approximation of the ideal conditions rather than an accurate measurement. Mite infestation levels were ideally set to zero.

Statistics

Regression analysis and statistical tests were performed using STATA v14. All variables were normalized by their mean value before regression analysis to avoid problems related with measurement units. The model was estimated in one stage with the use of an ordinary least square (OLS) regression procedure. Two alternative functional specifications (Cobb-Douglas and transcendental logarithmic) were initially considered for the approximation of the production function. The former is a special class of the latter that can be arrived at by imposing zero-order conditions on its parameters ($\beta_{bt} = \beta_{jt} = \beta_{bb} = \beta_{j\rho} = \beta_{bj},\ \forall j, \rho$). The Cobb-Douglas function was statistically tested against the transcendental logarithmic functional form using the log likelihood ratio test (LR test). Based on the testing results ($\chi^2 = 91.43$, $df = 20$, $p = 0.000$), the null hypothesis was rejected at the 1% significance level. Therefore, the *translog* functional specification was used to proxy the honey production technology. The LR test was also employed to statistically test three hypotheses with respect to the features of the honey production technology, namely, the hypothesis of constant returns to scale against variable returns of scale ($\chi^2 = 14.47$, $df = 3$, $p = 0.002$), no technical change against technical change ($\chi^2 = 7.98$, $df = 7$, $p = 0.334$) and *Hicks*-neutral technical change against factor-biased technical change ($\chi^2 = 2.35$, $df = 5$, $p = 0.799$). To consider possible effects of miticides, antibiotics, and feeding expenses on honeybee populations, all three productive inputs were additionally entered alone and interactively with neonicotinoids into the damage function. However, our estimation results did not generate significant coefficients for any of those terms. Hence, the productive inputs were not included in the specification of the damage function.

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