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Title

Impacts of honeybee density on crop yield: A meta-analysis

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Abstract

1. There is increasing recognition that pollination deficits are limiting crop yields worldwide. However, management strategies for optimal insect pollination are still unclear for most crops. Current management focuses on providing high densities of honeybees, but recommended densities are highly variable, even within single crops and cultivars.

2. We performed an extensive literature search to record honeybee densities (colony density and/or flower visitation rates) and crop productivity (fruit set, seed set, fruit weight, and/or yield). Effect sizes were represented as the difference in crop productivity between the two most extreme levels of honeybee densities.

3. Out of 795 reviewed studies, only 22 analysed the effect of at least two levels of honeybee densities on crop productivity (reporting 60 resulting effect sizes in total). Moreover, few recommendations for crop pollination management are based on results from controlled experimental designs, and with comparable methodology.

4. We found that both colony density and visitation rates increased all the productivity variables. However, effects were non-linear for visitation rates, suggesting that there is an optimum (mean of 8-10 visits per flower) beyond which more honeybees are not beneficial (or even detrimental) for crop productivity.

5. Effect sizes for visitation rates were greater than that for colony densities, suggesting that visitation rates are a more direct measure of the pollination process. Data on the relation between colony density and visitation rates are lacking. Interestingly, effect sizes for visitation rates were greater for crops with separate

sexes than those with hermaphroditic flowers; therefore, the benefits of honeybee pollination vary according to the crop biology.

6. *Synthesis and applications.* Current practices for crop pollination assume that more honeybees are always better for crop yield, even if the effect of this management on crop production still unclear. In contrast, our analyses suggest that there is an optimum for honeybee densities. Despite the importance of honeybees and pollinator-dependent crops worldwide, there is a lack of studies designed for finding such an optimal level of crop pollination. Our analyses further suggest that visitation rates could be used as a proxy to guide management recommendations such as colony density and spatial arrangement.

Second abstract (Spanish)

1. Los déficits de polinización están limitando la productividad de los cultivos en todo el mundo. Para sustentar el servicio de polinización en zonas de agricultura intensiva, el manejo actual consiste en saturar los cultivos de flores con abejas melíferas proveyendo altas densidades de colmenas. Sin embargo, se sabe muy poco sobre la eficiencia de este manejo para poder alcanzar una polinización óptima y existe controversia respecto las densidades recomendadas.
2. Realizamos una síntesis global de la literatura científica para registrar la densidad de abejas melíferas (tasa de visitas o densidad de colmenas) y la productividad de los cultivos (cantidad de frutos o de semillas por flor, peso del fruto, o rendimiento por

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hectárea o planta). Los tamaños de efecto se calcularon como la diferencia en la productividad entre los dos niveles más extremos de densidades de abejas.

3. De los 795 estudios revisados, solo 22 analizaron el efecto de al menos dos niveles de densidad de abejas sobre la productividad de los cultivos (resultando en 60 tamaños de efecto en total). Además, pocos estudios se basan en los resultados de diseños experimentales controlados y con una metodología comparable.
4. Encontramos que tanto la tasa de visita como la densidad de colmenas aumentaron todas las variables de productividad. Sin embargo, el efecto de la tasa de visita fue curvilíneo, lo que sugiere que hay un óptimo (8-10 visitas por flor) más allá del cual mas abejas no es beneficioso (o incluso perjudicial) para la productividad de los cultivos.
5. Los tamaños de efecto para la tasa de visitas fueron mayores que para la densidad de colmenas, lo que sugiere que la tasa de visitas es una medida más directa del proceso de polinización. Faltan datos sobre la relación entre la tasa de visitas y la densidad de colmenas. De modo interesante, el tamaño de efecto de la tasa de visitas fue mayor para cultivos con sexos separados que para aquellos con flores hermafroditas, lo que sugiere que los beneficios de la polinización por la abeja melífera dependen de la biología floral.
6. Síntesis y aplicaciones. El manejo actual para la polinización de los cultivos asume que más abejas siempre aumenta la productividad de los cultivos. En cambio, nuestros análisis sugieren que existe un óptimo para la tasa de visita de abejas y que

esa variable podría usarse como un proxy para guiar las recomendaciones de manejo, como la densidad de colmenas y su disposición espacial.

Keywords

honeybee colony density, visitation rate, crop yield, fruit set, seed set, fruit weight, pollination

Introduction

The European honeybee (*Apis mellifera* L.) is the foremost species used for crop pollination worldwide, both in open pollination (fields, orchards) and enclosed systems (Garibaldi *et al.* 2017). Honeybees have a large area of native distribution, generalist feeding behaviour (visit a large range of plants), high adaptability to a broad range of climatic conditions, and high tolerance to human management (Delaplane & Mayer 2000; Michener 2007). To maximize crop productivity, the goal is usually to saturate crop flowers with honeybee foragers provided by large numbers of colonies brought at the onset of flowering of the target crop (James & Pitts-Singer 2008).

Currently, there is no consensus on the optimal colony density to maximize crop yield, and recommendations are highly variable, even within the same crops and cultivars. Reference books on the topic (Free 1993; Delaplane & Mayer 2000) and certain other references (Le duc & Turcotte 2004; Department of Agriculture and Food 2006; Isaacs & Kirk 2010; Gaines-Day 2013; Howlett *et al.* 2015; Sheffield, Ngo & Azzu 2016; Cunningham *et al.* 2016) list a very large range of colony densities for various crops (Fig. 1). For example,

recommended honeybee densities for strawberries range from 2 to 25 colonies ha⁻¹ with values originating from several continents and no indication of pollination success. A similar range of variability is observed for blueberry pollination (1 to 25 colonies ha⁻¹). This range can be even more extreme, such as for onion cropping systems (from 2 to 37 colonies ha⁻¹). Even traditional crops with high economic value at the global scale like apples have unclear recommendations (ranging from 1 to 16 colonies ha⁻¹). Moreover, the recommended mean density of colonies can double between two species of the same genus, such as for sour cherry and sweet cherry (2.5 and 4.2 colonies ha⁻¹ respectively) or for clovers (3.7 and 7.7 colonies ha⁻¹ for respectively for *Trifolium repens* and *T.pratens*) (Delaplane & Mayer 2000). Thus, pollination is a multifaceted component of crop productivity and not easily reduced to applied recommendations. Furthermore, the recommended density of honeybees is difficult to synthesize because the literature is often scarce or incongruent, with strong fluctuations according to the crops, cultivars and spatial context.

It is generally assumed that more colonies increase pollination and crop productivity, but effects might be non-linear (e.g. asymptote or sigmoidal curves) (Delaplane & Mayer 2000; Steffan-Dewenter 2003; Morris, Vázquez & Chacoff 2010). Management strategy by saturation can result in an unusually high density of honeybees and may trigger drastic changes in local assemblages of wild insects (Mallinger, Gaines-Day & Gratton 2017). Such changes in species composition could increase interaction costs and reduce plant reproductive success and crop productivity (quantity and/or quality) (Hargreaves, Harder & Johnson 2009, 2010; Morris, Vázquez & Chacoff 2010; Aizen *et al.* 2014). Indeed, wild pollinators are a vital part of our crop systems (Garibaldi *et al.* 2013), and can improve pollination efficiency of honeybees (e.g. Brittain *et al.* 2013). However, wild bees are also

less abundant in large fields and show lower visitation rates and lower fidelity to individual plant species over time (Burkle, Marlin & Knight 2013), perhaps due to competition for resources with honeybees (Isaacs & Kirk 2010). In this context, it appears that combining controlled pollination services that use honeybee colonies with wild bee conservation strategies, by taking into account the levels of wild pollinators in the landscape, is important for ensuring stable pollination and sustainable crop yield. Other mechanisms by which high densities of honeybees can be detrimental to crop productivity include: when insect pollinators damage flowers during their visits or when a surplus of pollen deposition leads to stagnation of growing pollen tubes, as demonstrated both under experimental and natural conditions (Young 1988; Young & Young 1992; Morris, Vázquez & Chacoff 2010; Sáez *et al.* 2014). Therefore, increasing honeybee densities, through the introduction of a large quantity of colonies, does not necessarily ensure better crop productivity.

Furthermore, the relationship between the density of honeybee colonies and the resulting forager visitation rate to crop flowers remains largely unknown, and could even be non-linear. First, population dynamics and by consequence the forager quantity in one given colony depends on various biotic and abiotic factors, such as the quantity and quality of feeding resources in the landscape, colony reserves, viruses, and pathogens (Goulson *et al.* 2015; Dennis & Kemp 2016). Second, some mechanisms such as spillover or resource selection can modify the spatial distribution of honeybee foragers in the landscape (Tscharntke *et al.* 2012; Rollin *et al.* 2013; Holzschuh *et al.* 2016), thereby altering the response to the increase in colony density. We can suppose a lower effect of the increase of colony density on crop pollination and productivity if, for example, the foragers have stronger preferences for a floral resource other than the targeted crop in the landscape

(Blitzer *et al.* 2012). Third, a honeybee colony is not a standardized unit; colonies can vary around the world according to the number of bees, if it is a split colony or not, the stage in the colony dynamics (e.g. spring or summer; Russell, Barron & Harris 2013), and the type of hive (Crane 1999) with different structures (horizontal vs vertical), size of the hive body and number of frames in the hive body (Crane 1999). Moreover, pathogens and viruses can significantly change the colony dynamic and strength and reduce the number of workers compared to a healthy population of the same type of hive (vanEngelsdorp & Meixner 2010). Consequently, it becomes important to evaluate the effect of honeybee density on crop productivity (quality and quantity) of the major cropping systems around the world, through different ecological measures such as colony density and visitation rate, to permit a sustainable management of pollination services.

In this study, we examine the global effects of honeybee densities on crop productivity using a meta-analysis approach. Specifically, we asked: What is the effect of honeybee densities (as represented by colony density or flower visitation rates) on crop productivity (fruit set, seed set, fruit weight, and/or yield)? At which honeybee density do benefits for crop productivity level off? How do these benefits change for contrasting crops worldwide?

Materials and Methods

Study selection

For the meta-analysis, an extensive literature search was performed on the Web of Science, last updated in April 2017, using the search string "[honeybee* OR honeybee* OR *Apis mellifera*] AND [crop productivity* OR crop yield* OR yield gain* OR fruit set* OR fruit quality OR seed set* OR tube growth OR pollen deposit* OR visitation rate*]". As a result, a total of 793 studies were identified. Another literature search was performed using Google Scholar to access grey literature such as conference papers, reports, book chapters, but only two additional studies were found suitable. Abstracts and full-texts of these 795 studies were reviewed for relevance, using the following criteria:

- (1) Is it an empirical study of the effect of honeybee density on crop productivity?
- (2) Does it contain original results?
- (3) Does it contrast at least two levels of honeybee densities?
- (4) Does it measure any of the following variables: colony density, visits or abundance per flower, or the number of honeybees per plant?
- (5) Does it report honeybee impacts in terms of one or more of the following crop productivity measures: fruit set (fruit flower⁻¹), fruit weight (g fruit⁻¹), fruit length (cm), seed set (seeds fruit⁻¹), or yield (kg plant⁻¹ or kg hectare⁻¹)?

Studies selected in the Web of Science were identified by our keywords, but many used these keywords only to explain the context or discussion of the study, without analysing processes of honeybee pollination and/or crop productivity. Consequently, they were excluded from the meta-analysis. In addition, the measures of crop productivity needed to be based on pollination by honeybees. Moreover, honeybee densities had to be randomly assigned to experimental units (plots) in a controlled (manipulated) experiment such that differences among plots could be attributed to the experimental error and avoid biasing the results. Finally, some of the studies selected in the previous step had a specific methodology that did not permit us to combine and analyse data with the other ones (e.g. total number of foragers without surface unit, e.g. hectare or meter squared), and they were not included in the meta-analysis database, which covered, at this stage, 32 remaining studies, of which only 22 studies were included in the meta-analysis (see below).

Data collection and effect sizes

For each study, we recorded the mean and standard deviation (SD) for each crop productivity variable (i.e. response variables). Authors were contacted if the study design met our criteria but the data were not reported in a format suitable for our analysis. When a selected publication only presented their results graphically, we used Plot Digitizer (<http://plotdigitizer.sourceforge.net>) to obtain means and, if reported, sample variances (Thorn *et al.* 2017).

Each effect size represents the difference between two levels of honeybee densities (as measured by colony densities or flower visitation rates) on the crop productivity variable for one crop. When a study provided more than two levels of honeybee densities (which occurred in nine of the selected studies), we chose the two most extreme levels of these densities. The effect sizes were estimated separately for each year (Table 1). Indeed, most of the studies provided data for only one year (13 studies; see Table 1), thus mixed-effects models could not be applied (i.e. most random effects will be estimated with only one data point) and any possible influence of multiple years is small. Moreover, in some studies, different plots were sampled in different years. For comparing data across studies we calculated the effect size of the various response variables as the response ratios (R), analysed on a log unit (lnR) (Borenstein *et al.* 2009). A positive lnR value indicates higher crop productivity when honeybee densities increase, whereas a negative value indicates a decrease in crop productivity. A null value indicates no effect of the addition of honeybees on crop productivity.

Data analyses

We could estimate the effect sizes for 32 studies but only 22 studies were included in the quantitative analyses because there was not enough replication (at least 5 effect sizes) for the following metrics: number of honeybees per 100 flowers, number of colonies per field, visitation rate per tree, number of honeybee foragers introduced in the field, and number of honeybee visits per minute. Finally, the analyses included the effects of colony density (colonies ha⁻¹; e.g. Stern *et al.* 2004, 2005; Sapir *et al.* 2007) or flower visitation rate (visit flower⁻¹; e.g. Nicodemo *et al.* 2009; Artz & Nault 2011; Zhang *et al.* 2015) on fruit set (fruits

flower⁻¹), seed set (seeds fruit⁻¹), fruit weight (g fruit⁻¹) or yield (kg plant⁻¹) (Table 1). Mean and standard error are presented for each of these effects. We also tested through linear and non-linear (polynomial) regressions the influence of colony density on fruit set. The same analyses were performed to understand the influence of visitation rate on fruit set and seed set. Lack of replicates (at least 10 effect sizes) prevented similar analyses for other variables (see Table 1). For two of them, we also analysed the potential effect of the control level (lower level of the honeybee density for each effect size) as a predictor of the response ratio. We selected the best fit model according to the AIC.

To explain some of the variability in the effect sizes, we classified crops according to two traits expected to be relevant for pollination success, namely flower size and reproductive system (i.e. how female and male reproductive organs are distributed in individuals and flowers) (Fontaine *et al.* 2006; Garibaldi *et al.* 2015). Even if there are other plant traits as sources of variation (e.g. concerning the degree of self-incompatibility of geitogamy), we chose to use simple and known indicators, available for all the studied crop species. The flower size classification was realised by the measure of the widest part and defined as “small” (1–35 mm) or “large” (>35 mm) (see Garibaldi *et al.* 2015). The classification according to the reproductive system of the flower separated plants with “hermaphrodite flowers”, which present both male and female parts in the same flower, from plants with “imperfect flowers”, that is each flower presents only the female parts (pistil) or only the male parts (stamen). This category includes monoecious and dioecious plants (female and male flowers are present in the same individual or in separated individuals, respectively). However, for honeybee colony densities, the majority of the data came from plants with similar floral characteristics (out of 23 effect sizes, only 2 and 3 came

from crops with large and hermaphroditic flowers, respectively), thus preventing comparative statistical analysis. For visitation rates, we pooled data on fruit set and seed set, as they showed similar responses (see Fig. 2). This strategy increased the number of replicates for the analysis. We used t-tests to compare effect sizes for crops with contrasting flower sizes and reproductive systems. All the graphs and statistical analysis were computed using the R software version 3.4.2 (R Development Core Team 2017).

Results

After the selection according to our criteria, only 22 studies on 16 cropping systems were included in our meta-analysis (Table 1). For example, three studies could not be included because they only provided the yield or another metric for a specific quantity of colonies or foragers in the field (without a comparison with another density of honeybees). The selected studies are distributed across North America, South America, Europe, Africa, Asia and Oceania and the year of publication ranged from 1963 to 2014. A total of 60 effect sizes were found suitable for the meta-analysis.

Among the 16 crop species, kiwi was the most represented with three studies, apple, pear, pumpkin and watermelon by two studies, while all the other crop species by only one study (Table 1). The most used response variables were the fruit set (fruits flower⁻¹), seed set (seeds fruit⁻¹), yield (kg plant⁻¹) and fruit weight (g fruit⁻¹) with 33, 11, 8 and 8 effect sizes, respectively (Table 1). The observed values of colony density were between 0 to 6.8 colonies per hectare, with delta values from 0.18 to 6 added colonies per hectare. The observed values for visitation rate were between 0 to 25 visits per flower, for a tested

gradient from 1 to 24 added visits per flower. The maximum delta value for visitation rate was measured for an analysis of fruit set.

Globally, honeybees in the field, measured as colony density or visitation rate, increased crop productivity (Fig. 2). This occurred for all the crop productivity variables analysed. For fruit set, effect sizes were smaller for colony density than for flower visitation rate ($t = 5.19$, $p\text{-value} < 0.001$). Concerning the visitation rate, effect sizes were the same for seed set and fruit set ($t = -0.11$, $p\text{-value} = 0.91$). Effects sizes for fruit weight were smaller than those for fruit set ($t = 2.63$, $p\text{-value} = 0.016$) and seed set ($t = 1.95$, $p\text{-value} = 0.06$), but the latter trend was only marginally significant. Concerning colony density, effect sizes were similar for fruit set and yield ($t = 0.47$, $p\text{-value} = 0.65$) (Fig. 2). Effect sizes were not different between plants with large or small flowers ($t = 0.996$, $p\text{-value} = 0.32$), while we found a significant higher response ratio for plants with imperfect flowers (monoecious and dioecious plants) than with hermaphroditic flowers ($t = 2.28$, $p\text{-value} = 0.03$) (Fig. 3).

We found a positive linear relationship between fruit set and colony density. However, the relationship between fruit set and visitation rate was non-linear ($\Delta\text{AIC} = 3.0$), and a similar trend was found for seed set ($\Delta\text{AIC} = 6.6$) (Fig. 4). Interestingly, optimal levels of visitation rates (an increase of approximately 8-10 visits per flower) were similar for fruit set and seed set (Fig. 4). Moreover, the log response ratio of the fruit set was higher for an increase in the visitation rate than for the increase in colony density, up to 2.94 for the visit rate, versus 1.29 for the colony density. Furthermore, when included as a co-variable, the base level (i.e. the absolute density of the control) had no effect on the observed pattern both for the visitation rate ($p\text{-value} = 0.573$ and 0.844 on fruit set and seed set, respectively) and the colony density ($p\text{-value} = 0.073$).

Discussion

For many important crops, bee pollination translates into higher yield, higher seed or fruit quality, and faster fruit ripening (Fries & Stark 1983; ; Lindström *et al.* 2016). In our meta-analysis, we have shown a positive effect of honeybee densities (as represented by colony density or flower visitation rates) on crop productivity (fruit set, seed set, fruit weight, and/or yield). But this relationship seems to be non-linear for the visitation rate (maximum increase in crop productivity when the visit rate per flower is increased by 8-10 additional visits relative to the baseline). Despite the worldwide importance of crop pollination by honeybees, surprisingly few studies analyse this question testing a large gradient of honeybee densities. Moreover, there is huge variability across studies in the measures selected to quantify the impact of honeybees on crop pollination or productivity.

Non-linear responses

The relationship with the response ratio differed according to the observed predictive variable. The effects of visitation rate on fruit set or seed set were non-linear. Higher visitation rates increase fruit and seed productivity but after an optimal increase in the visitation rate (around 8 more visits per flower) this effect is smaller, becoming negative when the number of visits per flower increases by more than 22 visits (in the case of the fruit set). Some studies have shown or predicted a saturation and/or a significant decline in fruit-set with pollinator abundance, as for bumble bees (Sáez *et al.* 2014) or beetles (Young 1988), due to an increase in the ratio cost/benefit of insect pollination (Morris, Vázquez & Chacoff 2010). One explanation is that high visitation frequency can lead to cumulative damages of stigmatic surfaces or other female reproductive organs by repetitive contacts

(Sáez *et al.* 2014). Moreover, a surplus of pollen deposition leads to a stagnation of pollen grains or pollen tubes, which can interfere with each other and reduce the fertilization (Young & Young 1992).

In contrast, the relationship between colony density and fruit set seems to be linear and positive. One explanation could be that observed colony densities were not high enough to detect non-linear patterns in crop productivity. Indeed, the reviewed studies analyse gradients of colony densities smaller than those proposed in the literature for practical recommendations (compare colony densities in Fig. 4 to those in Fig. 1). For example, the recommendation for apple pollination ranges from 1 to 16 colonies per hectare (Fig. 1), but the colony densities used in the studies included in our meta-analysis ranged from 2.5 to 5 colonies per hectare (Fig. 4). Similarly, for cranberry, studies reviewed for the meta-analysis ranged from 0 to 7.4 colonies per hectare while the recommendation in the book by Delaplane & Mayer (2000) ranges from 1 to 22 colonies per hectare (however for cranberry, studies reviewed and selected after full-text assessment, were not finally included in the meta-analysis due to various problems with data quality). These observations confirm that we need studies with a greater gradient of colony densities and more replicates.

Effect sizes depend on flower reproductive traits

The effects of visitation rate on fruit and seed sets were higher for plants with imperfect flowers than for plants with hermaphroditic flowers (Fig. 3). Such differences in the response intensity might be tied to the degree of dependence of the plant on cross-

pollination by insects. This dependence varies with the level of self-fertility of the plant and the flower morphology (Delaplane & Mayer 2000). Generally, monoecious and dioecious plants are more dependent on insect pollination than hermaphroditic plants, and need insects, especially bees, as pollen vectors. In contrast, plants with hermaphroditic flowers generally have a higher degree of self-pollination (Morris, Vázquez & Chacoff 2010).

However, although the effect sizes on plants with hermaphroditic flowers is lower, the increase in honeybee visitation rate significantly increases crop productivity. Hermaphroditic flowers present a perfect structure to perform a full self-pollination. But to prevent inbreeding and promote genetic diversity, many species use cross-pollination and develop self-incompatibility mechanisms, such as temporal separation of the male and female phases (pollen production and stigma receptivity) (Barbier 1986; Delaplane & Mayer 2000; Rollin *et al.* 2016). For example, raspberry crops are fully self-fertile but the production of well-formed fruits depends on animal pollination (Cane 2005; Morales 2009; Sáez *et al.* 2014). Therefore, honeybee or bumble bee hives are commonly deployed in raspberry fields to ensure an adequate pollination (Velthuis & Doorn 2006; Garibaldi *et al.* 2017) and increase crop productivity.

Use of the visitation rate to adjust colony management

Honeybee densities in the crops were represented most frequently by counting colonies per hectare or visits per flower. We found greater effects sizes for visitation rate than for colony density. Visitation rates could be more relevant than colony density for several reasons.

First, density is only one measure of colony management. The spatial and temporal arrangements of the colonies can have different impacts on crop pollination and productivity. Indeed, colony density can be characterized as a function of the number of colonies per placement and the distance between each placement (see Cunningham *et al.* 2016). The percentage of flowers converted into fruit and the yield increases with colony density but decreases significantly when the distance from the crop to the colony placements increases (Manning & Wallis 2005; Cunningham *et al.* 2016). Moreover, some studies have shown the variability of the effect of a given colony density, according to multiple introductions of colonies for some crops like pear (Stern *et al.* 2004, 2005), apple (Stern, Eisikowitch & Dag 2001) and plum (Sapir *et al.* 2007). A sequential introduction of honeybee colonies enhanced bee pollination activity, with a higher honeybee visitation rate (bee min⁻¹ tree⁻¹). These multiple introductions can give the same or a higher fruit set and yield than a two times higher colony density with a single introduction. This point confirms that the relationship between crop productivity and colony density depends on other important management decisions.

Second, colonies can be very different in terms of quality and quantity of bees and can vary during the flowering season. For example, the size of a colony can vary greatly from 10.000 and 40.000 individuals across studies (10,000 in Hansted *et al.* 2015; 20,000 in Stern, Eisikowitch & Dag 2001; 25,000 in Walters 2005; 30,000 in Aras, De Oliveira & Savoie 1996; 40,000 in Quinet *et al.* 2016.) Another point concerns the plasticity of the working organisation in the colony to respond to environmental changes. Between 2 and 10 % of the total population size of the colony are available daily for foraging (Seeley 1985), usually the older individuals, because foraging is the last function of the worker (Menze *et al.* 2005).

But this percentage can show strong temporal variations (e.g. from 0 to 68% of the workers on a given day; Thom, Seeley & Tautz 2000), according to the quantity and quality of the reserves in the colony and the available pollen and nectar resources in the surrounding landscape (Beekman *et al.* 2004; Odoux *et al.* 2014). Moreover, some pathogens or viruses can cause damage in the population, or even the death of some colonies. So the number of bee foragers can vary greatly from one colony to another and their resistance to other environmental perturbations (climate, other pathogens and/or viruses, predators) can have various consequences on the composition and the dynamic of the population, and the colony survival (Delaplane & Mayer 2000).

Third, a higher number of colonies per hectare does not necessarily imply an increase in honeybee foragers in the field. Movements across habitats are a common phenomenon in many species. For their diet, honeybees forage on a wide diversity of floral resources spatially separated in the landscape, from both crops fields and non-cropped habitats (Odoux *et al.* 2012; Rollin *et al.* 2013; Requier *et al.* 2015) and need to make cross-habitat movements, including spillover from crops (where colonies are placed) to semi-natural habitats (Hanley *et al.* 2011; Blitzer *et al.* 2012; Tscharntke *et al.* 2012). Moreover, they can alter their foraging behaviour in response to the availability of floral resources in the landscape. They preferentially forage in the crop when alternative resources are scarce in the surrounding landscape, but they can move away from a crop to a semi-natural habitat if it presents a more attractive floral resource than the crop (Vaissiere 1991; Pettis *et al.* 2013; Gaines-Day & Gratton 2016). In this context, increasing the number of colonies in the landscape, and consequently, the number of honeybee foragers, does not necessarily signify a proportional increase of honeybee foragers in the targeted crop and higher pollination.

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Finally, the flower quantity per plant (or tree) can change with intra- and inter-annual variations. Especially in fruit crops (or tree crops), the density of flowers produced by plants, and therefore crop productivity, increases during approximately the first seven years and then stabilizes. Adult crops, at their maximal productivity level, can produce one or two orders of magnitude more flowers than when they began to produce. For this reason, some studies recommend different colony densities according to the age of the trees. For example, Delaplane & Mayer (2000) advise one colony per hectare for young peach trees and 2.5 colonies per hectare for older trees. In the USA in almond orchards, 2.5 colonies per hectare are placed during the first and second year of production because the trees are small. Then, it is advised to use 5 to 6.25 colonies per hectare (personal com. A. Sáez, 2017).

Thus, the recommended colony density depends on the attractiveness of the crop, the composition, abundance and attractiveness of the other competing floral resources in the landscape, the population density and composition of non-managed bees, the location and strength of honeybee colonies and other environmental variables like the climate. All these variables can result in strong variations in the density of honeybee foragers in the crop and consequently change the pollination success of honeybees and crop productivity. For these reasons, visitation rate rather than colony density would be a more precise measure for assessing the pollination service by honeybees.

However, routine management practices in bee pollination use the honeybee colony as a management unit, with beekeeper and farmer agreeing on a renting price per colony according to the pollinated crop, the pollination time, and the distance that the beekeeper must travel to drop off the hives at the field crop (e.g. websites to optimize communication between beekeepers and farmers for pollination service; <http://www.beewapi.com/>). Thus,

characterizing the relationship between colony density and crop productivity is very important, from the point of view of applied management and communication between beekeepers and farmers. Moreover, pollination services need standardized and strong colonies. The measure of field colony strength generally means population measures of adult bees and brood (i) by an observer at the beginning of a study or a pollination service to produce uniform colonies, or after an experiment, to evaluate a specific impact on the colonies, or (ii) by computer-assisted digital image analysis (Delaplane K.S., van der Steen J., Guzman-Novoa E. 2013). We can also use other indirect variables, such as drone brood production, queen cell production, comb construction, or flight activity at the entrance of the hive. For example, the ColEval method (Maisonnette et al., 2016) is based on the evaluation of the percentage of surface area occupied by five different components of the colony structure to determine colony performance: the number of bees, the amount of open brood and capped brood, the quantity of food (honey and nectar) and pollen. This method eliminates bias in the measurements between observers. Moreover, it also proposes, a posteriori an estimation of the number of honeybee foragers and, therefore, the potential pollination strength of a colony.

Developing these estimators is a key step in evaluating the link between colony strength, visitation rate and maximal pollination service. Once this relationship is characterized, we could compare the real visitation rate in one crop system with a theoretical optimal visitation rate and adjust the number of colonies and/or their placement (distance) to reduce or increase the observed visitation rate.

A lack of standardization

One of the major difficulties encountered in our meta-analysis was the lack of standardized methods and common metrics to analyse the impact of honeybees on pollination success or crop productivity. For example, honeybee management was measured as the number of colonies per hectare (Stern, Eisikowitch & Dag 2001; Stern *et al.* 2004, 2005), number of colonies per field (without information about field size) (Walters & Taylor 2006), number of introduced foragers (Fulton *et al.* 2015), number of bees per tree (for orchards) (Costa, Testolin & Vizzotto 1993), number of bees per tree per minute of observation (Sapir *et al.* 2007), number of bee visits per flower (Björkman 1995), number of bee visits per minute (Dedej & Delaplane 2003), number of bees per 100 flowers (Aras, De Oliveira & Savoie 1996) or number of bees per 100 m² (Evans & Spivak 2006). Similar complexity was observed for crop productivity, with studies measuring fruit set, number of fruits per 10 shrubs, yield per tree (in orchards), yield per 100 m², seed set, number of seeds per fruit, number of seeds per kg of fruit, fruit size (circumference), fruit length or fruit weight. Consequently, we found varying combinations of measures of honeybee density and crop productivity but with few replicates, which did not allow for comparison across studies and reduced the effective database (see Table 1). Future studies should follow more standardized reporting procedures to permit a statistical comparison between crops and environmental contexts. It is with this same objective that the Food and Agriculture Organization of the United Nations (FAO; <http://www.fao.org/home/en/>) published in 2011 a document to detect and measure pollination deficits in crops (Vaissière, Freitas & Gemmill-Herren 2011). This handbook presents a standardized protocol, and the modifications and applications of this protocol for a variety of circumstances in developing and developed countries, such as those with high

environmental variability and small fields. Some projects have started using this protocol and consequently, they will give comparable data (Garibaldi *et al.* 2016).

Synthesis and applications

Currently, the global demand for honeybee colonies for the pollination of fruit crops is growing (Aizen & Harder 2009). In various countries worldwide, this demand shows a more rapid growth than the number of colonies available for pollination (Aizen *et al.* 2008; Aizen & Harder 2009). Our study shows that both the visitation rate of honeybees and the number of honeybee colonies in the crops increase seed and fruit productivity worldwide. However, in contrast to current management assumptions (James & Pitts-Singer 2008; Garibaldi *et al.* 2017), the relationship seems to be non-linear for visitation rate. Current studies are not designed for finding such an optimal level of honeybee hive densities or honeybee visitation rates, and the relationship between colony densities and visitation rates is still unclear. These findings open new important avenues of research. Future studies should measure colony strength, and take into account crop pollination need and the presence of wild pollinators in the landscape of the considered crops to determine the optimal level of honeybee densities.

Authors' contributions

OR and LAG conceived the ideas, designed research, and wrote the manuscript; OR collected and analysed the data; OR and LAG interpreted the data. Both authors gave final approval for publication

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Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dj5f7kc>

(Rollin & Garibaldi 2019).

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Table 1. Details of the 22 studies included in the meta-analysis with the final number of studies and effect sizes used for each crop productivity variable. Each effect size represents the effect of the difference between two levels of honey bee densities (as measured by colony densities or flower visitation rates) on the crop productivity variable (log response ratio). When a study provided more than two levels of honey bee densities, we chose the two most extreme levels. Effect sizes were estimated separately for each year.

Study	Country	Crop	Year	Predictive variable	fruit set (fruit/flower ⁻¹)	seed set (seeds/fruit ⁻¹)	yield (kg/plant ⁻¹)	fruit weight (g/fruit ⁻¹)
Cunningham et al 2016	Australia	Almond	2012	Col /Ha	2			
Howpage et al 2001	Australia	Kiwi	1997	Col /Ha	1		1	
Rizzardo et al 2012	Brazil	Castor bean	2006	Col /Ha	1			
Sapir et al 2007	Israel	Plum	2003	Col /Ha	4		1	
Stern et al 2001	Israel	Apple	1997	Col /Ha	2		2	
Stern et al 2004	Israel	Pear	2001	Col /Ha	3		2	
Stern et al 2005	Israel	Pear	2002	Col /Ha	2		2	
Artz & Nault 2011	USA	Pumpkin	2008	Visit /flower	3	3		
Björkman 1995	USA	Buckwheat	1991	Visit /flower	3			
Chautá-Mellizo et al 2012	Colombia	Gooseberry	2010	Visit /flower		1		1
Garantonakis et al 2016	Crete	Watermelon	2014	Visit /flower		1		1
Garratt et al 2016	UK	Apple	2012	Visit /flower	1			
Goodwin et al 2013	New Zealand / Italia	Kiwi	2012	Visit /flower		1		1
McGregor et al 1965	USA	Cantaloups	1963	Visit /flower	1			
Miñarro & Twizell 2015	Spain	Kiwi	2013	Visit /flower	1			1
Nicodemo et al 2009	Brazil	Pumpkin	2001	Visit /flower	2	2		2
Pisanty et al 2014	Israel	Sunflower	2009	Visit /flower		1		

Romero & Quezada-Euan 2013	Mexico	Jatropha	2009	Visit /flower	1			1
Sampson & Cane 2000	USA	Blueberry	1999	Visit /flower	1	1		
Walters 2005	USA	Watermelon	1998	Visit /flower	1			
Witter et al 2015	Brazil	Oilseed rape	2012	Visit /flower	1	1		1
Zhang et al 2015	China	Peach	2012	Visit /flower	3			
# Contrasts					33	11	8	8
# Studies					18	8	5	7





