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The impact of honey bee colony quality on crop yield and farmers' profit in apples and pears

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ABSTRACT

Despite global interest in the role of pollinators for food production, their impact on farmers' profit, which determines farmers' livelihood and land-use decisions, is unclear. Although average values of pollinator benefits are generally assumed, there is potential for large spatial variation among crop species and varieties or among pollinator management strategies, even within the same region and year.

We studied how quality of honey bee colonies used for pollination services, which included artificial feeding during winter and pathogen control, affect flower visitation, fruit production, and farmers' profit in the main apple and pear producing region of Argentina (Patagonia).

For apple, high-quality colonies exhibited flower-visitation rates 130% greater than conventional colonies. Indeed, high-quality colonies increased fruit set by 15% (increasing production quantity), seed set and fruit sugar content, and subsequently farmeŕs profits by 70%. For pear, colony quality only affected fruit weight of the Abate Fetel variety, but not that of the Packham's Triumph variety. Fruits were ~20% heavier in farms deploying high quality colonies but did not contribute to increase farmers' profits to the extent that it did for apple.

In contrast to studies conducted elsewhere, we did not observe any wild pollinators visiting apple or pear flowers, highlighting the fragility of this conventionally intensified crop production system. We found that such orchard systems can suffer large pollinator deficits affecting farmers' profit. Given that *A. mellifera* was the only flower visitor, we could estimate the impact of improving colony management on farmer's profit without the influence of other pollinators. Our study also shows that variations within pome crops, *i.e.* apples and varieties of pears, in pollinator benefits can be very large, and that the assumption of global average values to guide local recommendations can be misleading.

1. Introduction

The ecosystem service of pollination might be threatened by ongoing pollinator decline (Goulson et al., 2015). Wild bee species, central to crop pollination (Garibaldi et al., 2011, 2013), have been declining in many parts of the world (e.g. Potts et al., 2010; Goulson et al., 2015). Although the global stock of domesticated honey bee colonies (*Apis mellifera*) has increased worldwide during recent decades (Aizen and Harder, 2009), demand for animal pollination has increased at a much higher pace (Aizen et al., 2008; Lautenbach et al., 2012). As a result, these disparate trends could lead to mismatches between demand and supply of pollination services (Breeze et al., 2014; Schulp et al., 2014). The benefits of agricultural intensification on entomophilous crop production might thus cease, or even turn into costs in the long run, because of a trade-off between agricultural intensification and adequate pollination service (Deguines et al., 2014; Garibaldi et al., 2016). Hence, there is an urgent need to develop a more sustainable agriculture by optimizing pollination and agricultural production while

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conserving biodiversity (Garibaldi et al., 2014). As a first step, the effectiveness of current pollination practices needs to be assessed.

Improving pollination through effective management can influence farmers' income through increased yield and yield stability of many food crops (Klein et al., 2007; Garibaldi et al., 2011). In addition to affecting overall yield, adequate pollination can also determine fruit and seed quality, including nutrient content (Eilers et al., 2011; Brittain et al., 2014). However, despite its widespread use as the prime managed pollinator for temperate fruit crops, the contribution of honey bees to fruit production, fruit quality and farmers' profits remain poorly known (*e.g.* Viana et al., 2014; Garratt et al., 2014; Marini et al., 2015). Understanding the dependence on honey bee pollination for yield and fruit quality is critical to develop managing strategies that enhance pollination and reduce temporal variability in production and farmers' profits (Garratt et al., 2014). However, there is a need to link pollination practices to a farmer's profit in order to assess the far-reaching consequences of pollination services (Garratt et al., 2014; Melathopoulos et al., 2015). So far, most studies have focused on the effect of different pollinator management schemes on yield quantity and quality, whereas only a few have addressed the economic consequences (*e.g.*, Kasina et al., 2009; Zhang et al., 2015). This lack of an economic dimension limits the usefulness of many of these studies to improve practices in different applied contexts (see Garibaldi et al., 2014 for a review).

Pears (*Pyrus communis*) and apples (*Malus domestica*) are economically major crops in Argentina, representing the first and third most exported fruit in 2012, respectively (Garcia-Sartor and Ulgade 2013). Both crops are insect pollinated and self-incompatible (Maccagnani et al., 2003; Ramírez and Davenport, 2013), and cross-pollination between different cultivars is needed to ensure high fruit set (Jackson, 2003). Several wild flower visitors are recognized as efficient pollinators of pears and apples, including bumble bees (*Bombus* spp.) and solitary bees (Maccagnani et al., 2003; Zisovich et al., 2012; Sheffield 2014; Földesi et al., 2016). In addition, several managed pollinator species, mostly *Apis mellifera*, are also routinely used to pollinate apple and pear orchards (Ramírez and Davenport, 2013).

We studied the effect of honey bee colony management, particularly colony preparation and health, on the pollination of apples and pears in Northern Patagonia. We developed an integrative approach to assess the consequences of honey bee colony management for both fruit quantity and quality, and address how the enhancement of these two yield components contribute to farmers' profits. We demonstrate that honey bee colony management is particularly critical in agroecosystems, particularly when alternative pollinators such as wild bees are absent.

2. Methods

2.1. Study sites

We conducted this study in the Alto Valle of Rio Negro and Neuquén, NW Patagonia, Argentina, from October 2014 to February 2015. The region of the Valle accounts for 75 and 85% of Argentinás pear and apple production, respectively. Within this region, we selected an area of 30 km long and 5 km wide (centered at approx. 38°37′ S, 68°18′ O) of 25-to–43 ha orchards with mixed apple and pear production lying within a river valley surrounded by typical shrubby vegetation of the Patagonian steppe. Orchards were conventionally managed making intensive use of herbicides (glyphosate), fungicides, and insecticides (neonicotinoids and organophosphates). A chemical thinning was applied to apple trees at the end of the fruiting season to cause the abortion of misshapen fruits. This treatment was not applied to pear trees as thinning hormones are naturally produced by pear trees. Orchard management practices (*e.g.* aspersion-irrigation) were similar among farms.

Within the study area, we selected a total of 37 apple and 51 pear trees, separated by at least 200 m and distributed across 88 different cultivated plots of similar size (*c.a.* 1.2 ha) nested within 22 different farms. To choose our focal trees, we focused on the Red Delicious (37 trees) apple variety, and Abate Fetel (25 trees) and Packham's Triumph (26 trees) pear varieties as those varieties were the most representative in this fruit-growing region. Packham's Triumph and Red delicious are self-incompatible and Abate Fetel is partially self-fertile (5–10% autogamy, Nyéki and Soltész, 2003). During the 2014 flowering season, the Abate Fetel variety was in bloom from September 6 to 17, Packham's Triumph from September 10 to 20, and Red Delicious from September 17 to 27. The number of different apple and pear varieties grown in each plot was counted as a proxy of cross-pollination potential.

2.2. Honey bee colony management

2.2.1. Colony characteristics

Orchards in the study area are usually supplemented with honey bee colonies at the onset of the flowering period of fruit trees. Farmers introduce honey bee colonies at a single location within the orchard or distribute one or two colonies per plot. In our study area, the mean prescribed density of colonies was 5 and 7 colonies$\cdot$ha^{-1} for apple and pear trees, respectively. We introduced this density of high-quality colonies in 10 of the 22 study orchards, and left the farmers to manage pollination using conventional colonies in the other 12 orchards. Unlike conventional colonies, high-quality colonies were prepared following a standardised protocol. First, queens were stimulated to start to lay eggs earlier by feeding colonies with sugar syrup directly after the winter. Second, health of each colony was carefully monitored upon delivery. These colonies were free of American and European foulbroods, and they had a rate of *Varroa destuctor* infestation $< 5\%$ (based on worker sealed brood) and were treated as necessary to maintain this health status. As a consequence, these colonies had a laying queen with a population of at least 20 000 bees when introduced into the orchards (based on the number of frames covered with bees; Vanengelsdorp et al., 2009).

During the flowering period of apple and pear trees (see above), we surveyed conventional and high-quality colonies once every week (in total 999 colonies were surveyed). At each survey, we counted the number of frames covered with bees as an estimation of colony strength (Vanengelsdorp et al., 2009). The number of frames covered with bees in conventional colonies was, on average, half that in high-quality colonies ($F = 133$; $P < 0.001$, mean ± sd = 4.6 ± 0.3 *vs.* 9.7 ± 1.1 for conventional and high-quality colonies, respectively; Fig. 1). These differences were reflected in the price a farmer had to pay for colony rental (5 US$ for a conventional colony and 20 US$ for a high-quality colony for the whole pollination season).

2.2.2. Colony density around the focal trees

We counted the number of colonies present in a 200 m radius plot around each focal tree as a proxy for the potential honey bee forager density. This distance was chosen because the activity of *A. mellifera* in cultivated fields declines drastically over a few hundred meters (Cunningham and Le Feuvre 2013; Cunningham et al., 2015). Specifically, a 200-m radius plot will encompass most of the foraging honey bee individuals that will potentially visit a given focal tree. In addition, for each focal tree we measured the linear distance (m) to the closest colony.

2.3. Visitation rates

During the flowering period of each variety, we conducted censuses of bee visitation to each of the 88 focal trees. We conducted a minimum of two and a maximum of five 10-min observation periods for each tree over its flowering period depending on logistics and weather conditions, totalling 259 10-min censuses on the 88 focal trees. At the beginning of each census, we counted the number of open flowers on five

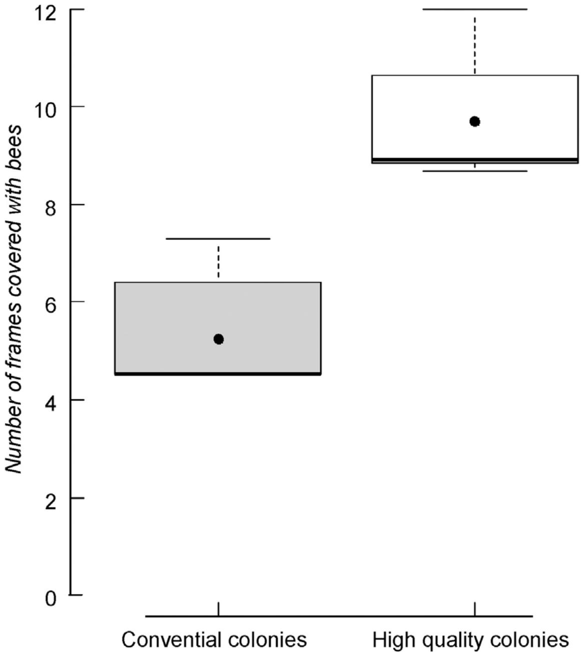

Fig. 1. Difference in colony size between conventional (light-grey) and high-quality (white) colonies. The black line in the box represent the median, the black point the mean. The bottom and top limits of each box are the first and third quartiles, respectively (black lines).

tagged branches·tree^{-1} and recorded the number of flowers visited by each floral visitor during the ensuing period. A mean ± sd of 112 ± 21, 145 ± 46, and 72 ± 15 flowers·tree^{-1} were observed on Abate Fetel, Packham's Triumph and Red Delicious, respectively. We thus obtained a visitation rate (number of visits· flower^{-1}·minute^{-1}) for each tree. We observed some feral honey bee colonies in our orchards, but were unable to discriminate between honey bees from managed or feral colonies, so all visits made by *A. mellifera* were pooled.

2.4. Fruit quantity and quality

2.4.1. Fruit set

In February 2015, at the end of the period of natural thinning for pears and chemically-induced thinning for apples, we counted the number of fruits produced on each focal tree. We estimated the total number of fruits·tree^{-1} by counting the number of fruits in the 5 tagged branches (the same ones used to assess flower-visitor visitation rate) and by multiplying the mean by the number of branches·tree^{-1}.

2.4.2. Fruit quality

We harvested all fruits produced by the five tagged branches monitored during the flowering period and assessed the quality of those fruits. As estimates of fruit quality, we measured fruit size (circumference, max width, height, and fresh weight), counted the number of carpels with seeds (0–5), and determined sugar concentration of the flesh. Fruit circumference at its maximum width was measured with a tape-measure, width and height using a calliper to the nearest 0.1 mm, weight by means of a digital balance sensitive to the nearest 0.01 g, and sugar concentration (in Brix) using a portable refractometer.

2.4.3. Farmer's profit

From March to November 2015, we obtained weekly wholesale values for apples and pears at the closest reference markets (http://www.idr.org.ar/?cat = 154; 2016). The price depended on the quality of the fruit which was estimated by its individual weight (x) as categorized in three classes for apples (small: $x \leq 130$ g at $0.38\ \mathrm{US\$.kg^{-1}}$; medium: $130 < x \leq 170$ g at $0.66\ \mathrm{US\$.kg^{1}}$; large: $x > 170$ g at $0.80\ \mathrm{US\$.kg^{-1}}$) and two for pears (small: $x \leq 150$ g at $0.27\mathrm{US\$.kg^{1}}$;large: $x > 150$ g and $0.53\mathrm{US\$.kg^{-1}}$). Production costs (agrochemicals, salary, gasoline, etc., rental of honey bee colonies excluded) average $0.28\ \mathrm{US\$.kg^{-1}}$ for apples and $0.18\ \mathrm{US\$.kg^{-1}}$ for pears (A. Mussi, *pers. com.*). On average, 70% and 80% of pear and apple production were sold, respectively (A. Mussi, *pers. com.*).

For each fruit crop, we estimated a farmer's profit in $\mathrm{US\$.ha^{-1}}$ as follows:

$$Prof.\ apples = (w{*}f{*}d{*}c{*}0.8) - (col{*}p) - (w{*}f{*}d{*}0.8{*}0.28)$$

$$Prof.\ pears = (w{*}s{*}f{*}d{*}c{*}0.7) - (col{*}p) - (w{*}d{*}0.7{*}0.18)$$

where

w = mean weight of fruits harvested.tree^{-1};
f = total number of fruits.tree^{-1};
d = number of trees.ha^{-1};
c = price category based on fruit's weight;
col = stocking rate of colonies.ha^{-1} (*i.e.* 5 and 7 colonies/ha for apple and pears, respectively); and
p = rental price per colony (*i.e.* 5 and 20 US$ for a conventional and high quality colony, respectively).

As in Delaplane et al. (2013), we calculated the marginal benefit for farmers (the difference in profit) due to the increase in the quality of bee colonies (ΔP), as follows:

$$\Delta P = Prof.HQ - Prof.Conv$$

where *Prof.HQ* and *Prof.Conv* was the profit ($\mathrm{US\$\ ha^{-1}}$) of a farm supplemented with high-quality and conventional colonies, respectively.

2.5. Statistical analyses

We built a cause-effect model (see an example regarding apple trees in Fig. 3) to test how honeybee colony management translated into flower visitation rate, which in turn affected fruit set and fruit quality. To evaluate the effect of colony management, we took into account three variables: a) honey bee colony density in a 200 m radius, b) distance between a focal tree and the closest colony, and c) colony quality (conventional *vs.* high quality). The number of flowers·tree^{-1} was taken into account as an estimation of the attractiveness of a tree. We also considered the number of tree varieties in each plot to evaluate the potential for cross-pollination. Fruit quality was evaluated as a) the number of seeds.fruit^{-1} which is related to pollination quality; b) sugar content and c) individual fruit weight, which is a critical factor in the economic valuation of the production and was also highly correlated to fruit circumference, width, and length (data not shown).

We used a cause-effect path analysis model, a statistical tool frequently used in ecology to test causal hypotheses between variables (Shipley, 2009). Classical path analysis does not take into account multi-level data (*e.g.* with random effects such as mixed-effect models). However, our model contained multi-level data because several trees belonged to the same farm, and thus the farm factor needed to be considered as a random factor in our models. To solve this problem, Shipley (2009, 2013) developed an alternative procedure for conducting path analysis that allows consideration of the hierarchical structure of the data called "Generalized multilevel path analysis". Briefly, this test first identified all k possible "missing paths", which are all the variables not linked directly and thus expected to be statistically independent. As an example, if A causes B and B causes C, the missing path (k) is the direct effect of A on C. Then, the test includes the calculation of the probability (P_i) that A has no direct effect on C *after* accounting for the effects of A on B and B on C. To validate any proposed path analysis, the combined probability of all missing path (k's) of the path diagram is thus calculated according to:

$$C = -2\sum_{i=1}^{k} ln(Pi)$$

The C statistics has an approximated $\chi2$ distribution with 2k degrees of freedom (Shipley 2009, 2013). The path model is rejected if the *P* value is < 0.05, which means that a direct effect of A on C still exists despite the controlled indirect effect of A on C through B.

To construct our model implementing Shipley's approach, we checked for multicollinearity between our chosen variables using the Variance Inflation Factor. Then, all variables were standardised using *Z*-scores. Finally, following the procedure described in the Piecewise Structural Equation Modelling package, (Lefcheck, 2016; V. 3.2.2, R Development Core Team, 2015), we constructed the models associated to each of the path proposed in Figs. 3, 5 and 6 using linear mixed-effect models. The normal-distribution of residuals of each test was checked. The Piecewise Structural Equation Modelling package runs Generalized multilevel path analyses (Shipley 2009, 2013) and provides an estimation and statistical significance of the C statistic, its magnitude and the direct effect for all variables (estimates of variables connected by an arrows and their *p*-values).

Finally, we analysed the effect of colony quality on farmers' profits for pear and apple. To achieve this goal, the differences in profit between orchards with high- vs conventional colonies for these two fruit crops were compared with a non-parametric Wilcoxon-test. We estimated *ΔP* when the Wilcoxon-test was significant.

3. Results

3.1. Visitation rate

During the 259 pollinator censuses, we recorded a total of 1059 pollinator visits to apple and pear flowers. All visits, except one by a syrphid fly to the flowers of a Packham's Triumph pear tree, were done by *A. mellifera*. We observed no wild bees in the orchards in almost two months of observation during the pear and apple flowering. Therefore, pollination of these fruit crops relies uniquely on *A. mellifera*. Visitation rate was significantly higher in apple than in pear flowers with a mean ± CI95% of 0.80 ± 0.17 and 0.24 ± 0.08 visits for 100 flowers.min^{-1} for apple and pears flowers, respectively (W = 259, $P < 0.001$; Fig. 2).

3.2. Apple

The generalized multilevel path model for apple trees explained our data adequately (Fisher's $C = 40.04$, k = 29, $P > 0.05$). Fig. 3 presents the path diagram we tested and Table 1 presents estimates of all the direct effects and the corresponding *p*-values. Most notable was the positive significant effect of colony quality on bee visitation rates (estimate = 0.76, SE = 0.16, $P = 0.001$, Fig. 4a). In turn, visitation rate had a significant positive effect on the number of fruits.tree^{-1} (estimate = 0.23, SE = 0.11, $P = 0.04$, Fig. 4b), the number of seeds.fruit^{-1} (estimate = 0.49, SE = 0.14, $P = 0.003$), and pulp sugar concentration (estimate = 0.44, SE = 0.15, $P = 0.007$, Fig. 3c). However, while both fruit quantity and quality increased with increasing bee visitation, a higher fruit load at the tree level resulted in diminished sugar concentration (Estimate = −0.77, SE = 0.17, $p < 0.001$, Fig. 4d) and individual fruit weight (Estimate = −0.85, SE = 0.18, $p < 0.001$, Fig. 4e).

Results on the economic valuation highlight a significant increase in profit for farmers that rented high-quality *vs.* conventional colonies (W = 66, $P = 0.043$, Fig. 4f). The mean net profit for farms that used high-quality colonies was 17 540 ± 11 195 US$/ha (mean ± SE), whereas for farms supplied with conventional colonies it was only 10 260 ± 7 087 US$/ha (mean ± SE). The marginal benefit (i.e *ΔP*) for farmers who used high-quality colonies thus amounted to 7 280 US $/ha.

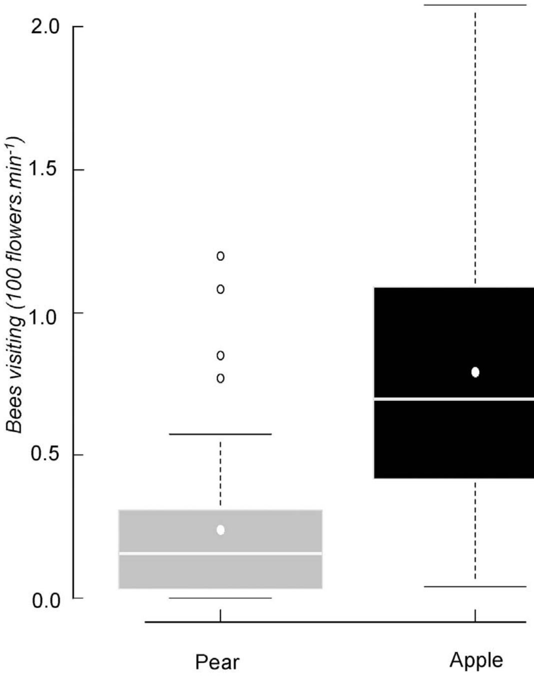

Fig. 2. Visitation rate for pear (grey) and apple (black) trees. The white line in the box represents the median, the white point the mean. The bottom and top limits of each box are the first and third quartiles, respectively (black lines).

3.3. Pears

3.3.1. Packham's triumph

The proposed generalized multilevel path model for trees of pear's Packham's Triumph variety fitted the data adequately (Fisher's $C = 39.86$, k = 30, $P > 0.05$, Fig. 5). However, the number of fruits per tree was related significantly to the number of flowers.tree^{1} only (estimate = 0.51, SE = 0.22, $P = 0.044$). Colony management, including density within a 200 m radius plot around a focal tree and colony quality, did not have a significant effect on visitation rates (Table 2). As a consequence, we did not detect any effect of colony quality on farmers' profit (W = 86, $P = 0.56$).

3.3.2. Abate fetel

The proposed generalized multilevel path model for trees of the Abate Fetel variety of pears fitted the data adequately ($C = 46.56$, k = 36, $P > 0.05$, Fig. 6). Colony quality had a significant effect on individual fruit weight (estimate = 0.48, SE = 0.19, $P = 0.037$, Fig. 7a, Table 3), but as for apple there was also a trade-off between number of fruits/tree and individual fruit weight (estimate = −0.39, SE = 0.16, $P = 0.031$, Fig. 7b). Like Packham's Triumph, colony quality did not have a significant influence on a farmer's profit in this variety either (W = 75, $P = 0.99$).

4. Discussion

We examined if management improvements of honey bee colonies used for pollination can improve fruit production, and found that colony quality enhanced honey bee visitation, increased the number of fruits/tree and sugar content as well as overall farmers' profit for apples, although for pears, this effect was only found for the weight of the Abete Fetel variety. This study also highlights the extreme fragility of the production of pears and apples in this area because of its exclusive reliance on a single species, *A. mellifera*, for pollination. This could be taken as a case study for crop pollination under a scenario of extreme wild bee decline.

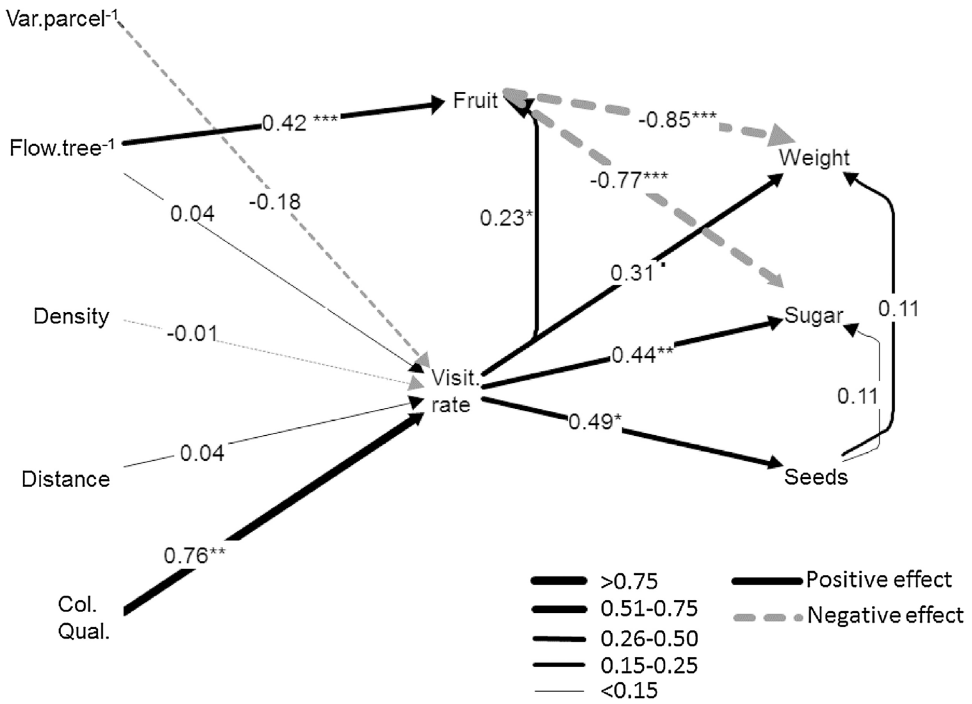

Fig. 3. Generalized Multilevel Path Analysis for apple trees. The thickness of an arrow represents the magnitude of the effect, which is also provided. The arrow and the sign of estimates shows if correlation is positive (black) or negative (dotted grey). ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. ˙$P < 0.1$. Var.parcel^{-1}: no. of varieties per parcel; Flow.tree^{-1}: calculated number of flowers per tree; Col qual: Colony quality; Density: colony density in a 200 m radius; Fruit: number of fruits.tree^{-1}; Visit. rate: visitation rate.

4.1. Managing honey bees to improve colony quality

The most common pollinator management practice for farmers to reduce pollination deficits is to increase the number of honey bee colonies, which increases production costs. However, stocking a field with more colonies does not necessary result in higher fruit production (*e.g.,* Viana et al., 2014). Our results clearly show that colony quality rather than quantity is a critical factor to improve pollination (in our case, the colony density around trees in a 200 m radius was, on average, 16.5 ± 15 colonies). Because conventional colonies are rented at a low price (5 US$ for the pollination season), beekeepers do not manage these colonies to maintain them in good health. As a result, conventional colonies had, on average, about half the number of workers compared with high-quality colonies (11 000 *vs.* 20 000 workers, see Fig. 1). In addition, the conventional colonies often had sanitary problems, with high infection rates of *Varroa* mites, which means weaker and probably less active workers.

4.2. Quality colonies enhance apple fruit production and farmers' profits

The use of high quality colonies in orchards increased the number of apples.tree^{-1} produced. For apple flowers, bee visitation rates

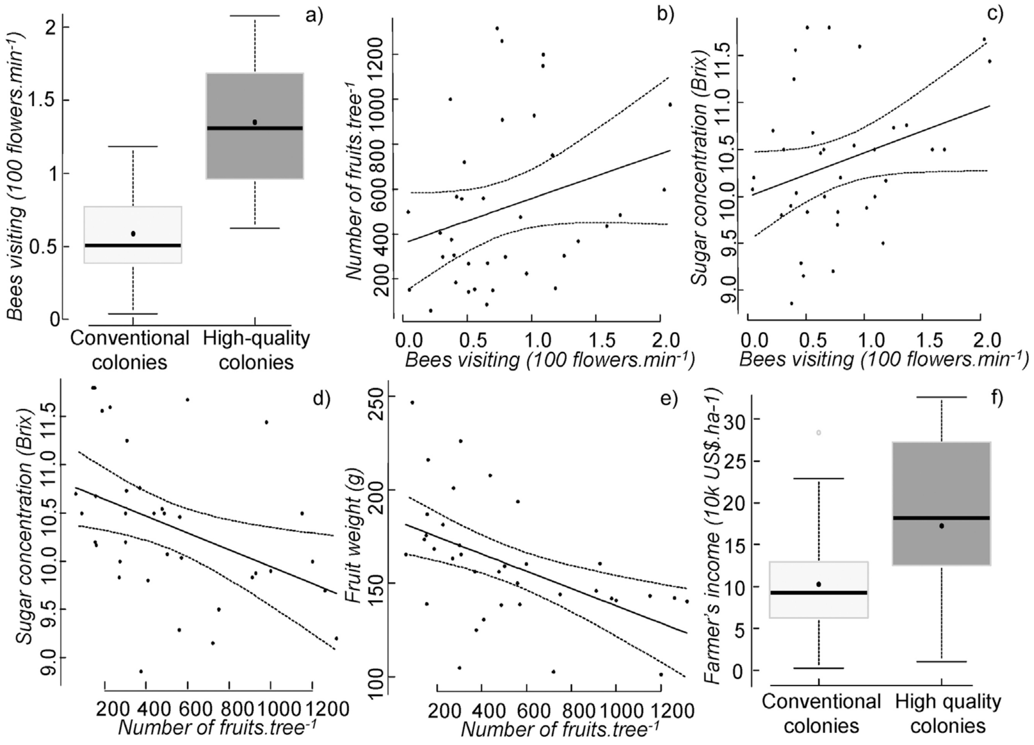

Fig. 4. Effects of colony quality, visitation rate and fruit load on visitation, fruit quality and farmers' profit in apple. a) Effect of colony quality on the visitation rate (visits/100 flower/min) in farms with conventional (light-grey) and high quality (dark-grey) colonies. b) Fruit load per tree in relation to the visitation rate of honey bees (100 bees.flower^{-1}.minute^{-1}). c) Sugar concentration in apples (BRIXSI unit) in relation to the visitation rate of honey bees (100 bees/flower/min). d) Sugar concentration in apples (BRIX) in relation to the fruit load per tree. e) Individual apple weight (g) in relation to the fruit load per tree. f) Effect of honey bee colony quality on the gross income (1000 US$.hectare^{-1}) for farms with conventional (light-grey) and high quality (dark-grey) colonies. For a) and f) the black line in the box is the median, the black point the mean; the bottom and top limits of each box are the lower and upper quartiles, respectively (black lines). For b), c), d) and e), the line in black is the estimate of the linear model, dotted-lines are the 95% Confidence Intervals.

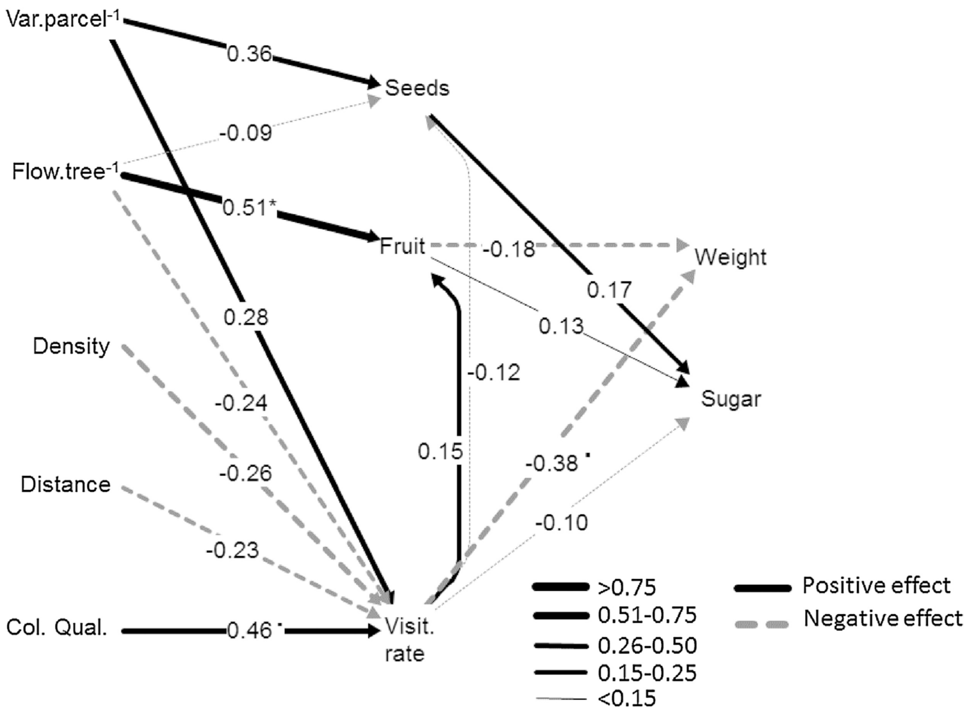

Fig. 5. Path diagram tested with the Generalized Multilevel Path Analysis for Packham's Triumph pear variety. The thickness of an arrow represents the magnitude of the effect, which is also provided. The colour of the arrow and the sign of estimates shows if correlation is positive (black) or negative (dotted grey). $***P < 0.001$, $**P < 0.01$, $*P < 0.05$. $\cdot P < 0.1$. Var.parcel^{-1}: No. of cultivated varieties per parcel; Flow.tree^{-1}: no. flowers per tree; Col qual: colony quality; Density: colony density in a 200 m radius; Fruit: fruits.trees^{-1}; Visit. rate: visitation rate.

increased and subsequently improved the number of fruits produced and their quality. In general, higher bee density might enhance bee movement, increasing as a consequence, flights between trees, and promoting cross-pollination (Garratt et al., 2013) and thus fruit production.

Several studies have shown that well-pollinated apple flowers result in higher seed set and better nutritional fruit quality (Buccheri and Di Vaio, 2005; Sheffield et al., 2005; Matsumoto et al., 2012). Our results corroborate those findings, as we found that visitation increased the number of fruits, number of seeds/fruit, and flesh sugar concentration. However, high fruit set can have negative implications for fruit quality because high fruit loads can negatively affect individual apple size and weight (Volz et al., 1996; Garratt et al., 2013). Indeed, due to plant resources allocation trade-offs (see Wesselingh (2007) for a review), excessive apple fruit production can lead to smaller fruits of lower quality, although fruit thinning usually alleviates this problem (see also Garratt et al., 2013).

Our results have direct implications for farmers' profits. We estimated that the mean *net* profit for farmers, averaged over all the studied apple orchards, was 12 080 US$/ha. However, we observed an important profit difference (*ΔP*) depending on colony quality (Fig. 3f) of more than 7000 US$/ha for orchards with high-quality *vs.* conventional

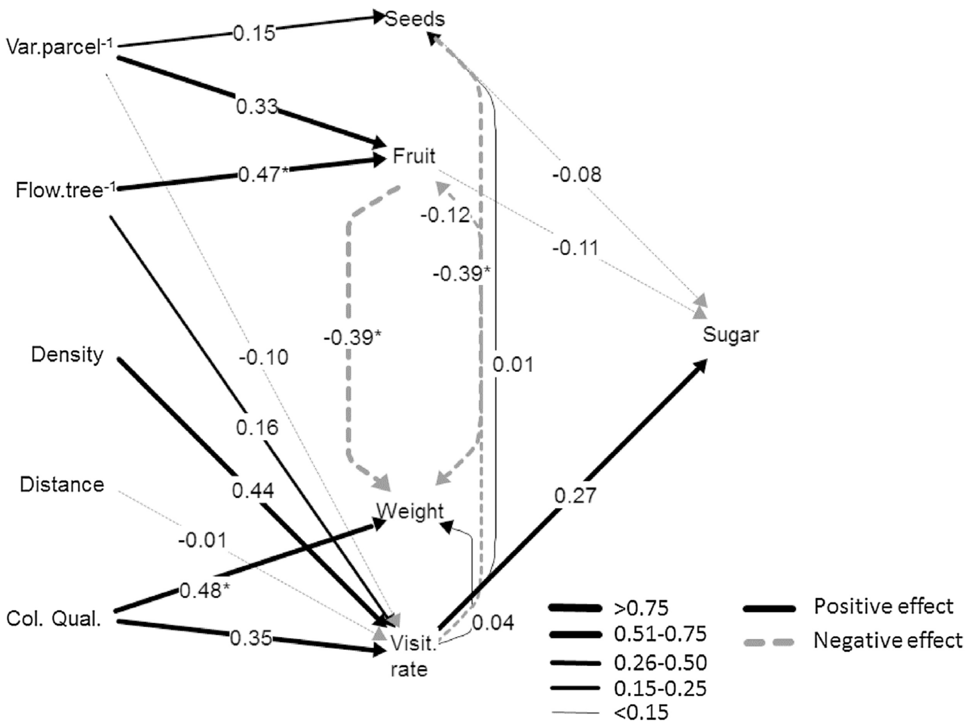

Fig. 6. Path diagram tested with the Generalized Multilevel Path Analysis for Abate Fetel variety. The thickness of an arrow represents the magnitude of the effect, which is also provided. The colour of the arrow and the sign of estimates shows if correlation is positive (black) or negative (dotted grey). $***P < 0.001$, $**P < 0.01$, $*P < 0.05$. $\cdot P < 0.1$. Var.parcel^{-1}: Variety per parcel; Flowtree^{-1}: flowers per trees; Col qual: Colony quality; Density: colony density in a 200 m radius; Fruit: number of fruits.tree^{-1}; Visit. rate: visitation rate.

Table 1
Results of the Generalized Multilevel Path Analysis for apple trees. Var.parcel^{-1}: no. of varieties per parcel; Density: colony density in a 200 m radius; Flow.tree^{-1}: flowers per tree; Col qual: colony quality; Fruit: number of fruits.tree^{-1}; Visit. rate: visitation rate.

Generalized Multilevel Path Analysisfor apple trees	
Fisher.C	40.04
P. Value	> 0.05
n	36

Path No.	Response	Predictor	Estimate	std.error	p.value
1	Visit. rate	Qual. Col.	0.76	0.16	0.0011
2	Visit. rate	Var. parc.	−0.18	0.15	0.2414
3	Visit. rate	Flow. Tree	0.04	0.13	0.7422
4	Visit. rate	Distance	0.04	0.22	0.8682
5	Visit. rate	Density	−0.01	0.18	0.9502
6	Fruit	Flow. Tree	0.42	0.11	0.0007
7	Fruit	Visit. rate	0.23	0.11	0.0402
8	Seeds	Visit. rate	0.49	0.14	0.0028
9	Sugar	Fruit	−0.77	0.17	0.0002
10	Sugar	Visit. rate	0.44	0.15	0.0069
11	Sugar	Seeds	0.11	0.13	0.3980
12	Weigth	Fruit	−0.85	0.18	0.0001
13	Weigth	Visit. rate	0.31	0.16	0.0623
14	Weigth	Seeds	0.11	0.15	0.4806

Table 2
Results of the Generalized Multilevel Path Analysis for Packham's pear trees. Var.parcel^{-1}: no. of varieties per plot; Density: colony density in a 200 m radius; Flow.tree^{-1}: flowers per tree; Col qual: colony quality; Fruit: number of fruits.tree^{-1}; Visit. rate: visitation rate.

Generalized Multilevel Path Analysis for Packham's trees	
Fisher.C	39.86
P. Value	> 0.05
n	25

Path No.	Response	Predictor	Estimate	std.error	p.value
1	Visit. rate	Distance	−0.23	0.19	0.2567
2	Visit. rate	Density	−0.26	0.21	0.2352
3	Visit. rate	Var. parc.	0.28	0.25	0.3033
4	Visit. rate	Flow. Tree	−0.24	0.24	0.3343
5	Visit. rate	Qual. Col.	0.46	0.23	0.0713
6	Fruit	Visit. rate	0.15	0.2	0.4695
7	Fruit	Flow. Tree	0.51	0.22	0.044
8	Seeds	Visit. rate	−0.12	0.17	0.4884
9	Seeds	Flow. Tree	−0.09	0.22	0.7098
10	Seeds	Var. parc.	0.36	0.26	0.1912
11	Sugar	Visit. rate	−0.1	0.15	0.5505
12	Sugar	Fruit	0.13	0.17	0.4568
13	Sugar	Seeds	0.17	0.2	0.3943
14	Weight	Visit. rate	−0.38	0.2	0.0862
15	Weight	Fruit	−0.18	0.2	0.4019

colonies. This large income difference thus reflects a strong pollination deficit for conventionally-managed orchards. This difference exists despite the higher cost of renting high-quality colonies from beekeepers (75 US$/ha), demonstrating that a relatively small investment to boost pollination services and reduce pollination deficits could result in very large marginal profits. Garratt et al. (2014) estimated the profit for the Cox apple variety at 19 600 £/ha (~28 000US$/ha) in the English market, but taking into account solely thinning costs. Also, pollination services in the study of Garratt et al. (2014) relied on a more diverse bee assemblage than solely *A. mellifera* as in our study, which may highlight that, even with the deployment of high-quality colonies, there may still exist a pollination deficit in our orchards. Furthermore, investment in well-managed colonies might also lead to a virtuous cycle with higher profits for beekeepers because of the higher price of rents. Thus, colony management could also improve collaborations between farmers and beekeepers.

Surveys to assess colony strength should be incorporated in farmers' practices to optimize pollination services. This finding should also serve to encourage future studies on pollination services to not focus solely on optimal stocking rates of honey beecolonies (see also Viana et al., 2014).

4.3. Honey bees, pear pollination and fruit production

In contrast to apple, bee colony quality was mostly unrelated to pear production. Our results showed that colony quality was solely related to an increase in mean individual fruit weight in the Abate Fetel variety. Pear flowers are less attractive to honey bees because, compared to flowers of other species in the Rosaceae, they secrete a very limited amount of nectar (Farkas and Orosz-Kovács, 2003) of low sugar concentration (Maccagnani et al., 2007, Fig. 2). As a consequence, honey bees usually switch to more attractive floral resources when available (Free, 1993; Zisovich et al., 2012). This may be one of the reasons why we often recorded many censuses with zero honey bee visit and a reduced range in visitation rates. Furthermore, Stern et al. (2004, 2007) showed that increasing the stocking rate of honey bee colonies just at the onset of orchard flowering is not effective for pear pollination. Instead, they showed that introducing colonies sequentially and increasing their numbers along the flowering period improved the number of honey bees foraging on flowering pear trees and their mobility among rows, which resulted in increased fruit set. Such a management technique remains to be evaluated in Argentinian pear orchards and might be more effective to reduce pollination deficit than only increasing either the colony quantity or quality with a single date of colony delivery.

In addition, rather than just managing only honey bees, the reintroduction of wild pollinators within pear orchards might also mitigate pollination deficits (Garibaldi et al., 2016). For example, *Osmia* (Maccagnani et al., 2007) and bumble bee species (Zisovich et al., 2012) are known to be efficient pollinators of pear flowers. Finally, plant breeding system should be considered in how much effort should be invested in managing pollination service. For instance, the Abate Fetel variety exhibits some level of self-fertility (Nyéki and Soltész, 2003), which might reduce its overall dependence on pollinators.

4.4. Dependence on honey bees for pollination

Pear and apple orchards have been shown to support relatively diverse communities of wild bees in agroecosystems elsewhere in the world (> 100 species recorded in Russo et al., 2015; Kammerer et al., 2016; 85 in Mallinger et al., 2016). Here, we did not observe wild bees visiting apple or pear flowers in orchards in NW Patagonia. Hence, pollination in this system relies solely on *A. mellifera*. This is, however, similar to Australian almond orchards, where insect pollination also relies exclusively on honey bees (Cunningham et al., 2015). A complete dependency on a single species for pollination is risky as, in case of honey bee colony shortage, the number of fruits can be greatly reduced. One clear example is provided by Californian almond, where farmers had to import colonies from Australia in 2005 to pollinate this crop (Klein et al., 2007). Furthermore, wild bees are, on average, more effective crop pollinators than honey bees (Garibaldi et al., 2013; 2016). Recent studies have shown that pollination success in apples was significantly more related to wild bee species richness than to honey bee abundance (Mallinger and Gratton 2015; Földesi et al., 2016). Indeed, the per-visit performance of several wild bee species has been shown to be greater than that of the honey bee for the pollination of rosaceous species (Thomson and Goodell 2001). Some bee species such as bumble bees might be more efficient because they can forage at lower temperatures than honey bees, or improve indirectly the effectiveness of honey bees by enhancing their mobility between trees rows and thus

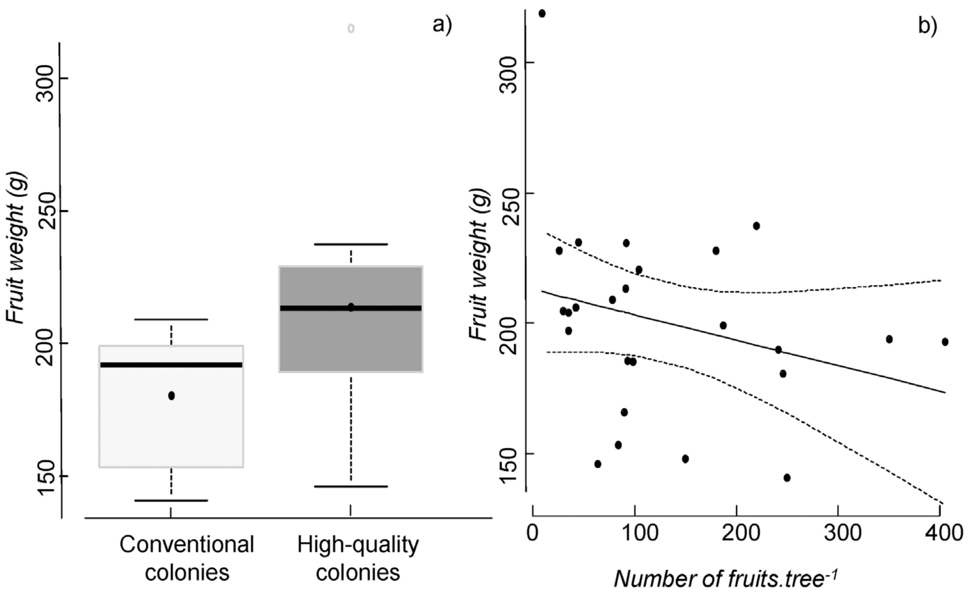

Fig. 7. a) Effects of honey bee colony quality on fruit size in Abate Fetel pears. The black line in the box represent the median, the black point the mean; the bottom and top limits of each box are the lower and upper quartiles, respectively (black lines). b) Individual fruit size in relation to the fruit load. The line in black represents the estimate of the linear model, dotted-lines are the 95% Confidence Intervals.

Table 3
Results of the Generalized Multilevel Path Analysis for Abate Fetel pear trees. Var.parcel^{-1}: no. of varieties per plot; Density: colony density in a 200 m radius; Flow.tree^{-1}: no. of flowers per tree; Col qual: colony quality; Fruit: Number of fruits per tree; Visit. rate: visitation rate.

Generalized Multilevel Path Analysis for abate trees					
Fisher.C			46.56		
P. Value			> 0.05		
n			25		
Path No.	Response	Predictor	Estimate	std.error	p.value
1	Visit. rate	Qual. Col.	0.35	0.29	0.2596
2	Visit. rate	Distance	−0.01	0.28	0.9825
3	Visit. rate	Density	0.44	0.27	0.1314
4	Visit. rate	Var. parc.	−0.1	0.25	0.7002
5	Visit. rate	Flow. Tree	0.16	0.22	0.4807
6	Fruit	Visit. rate	−0.13	0.19	0.5031
7	Fruit	Flow. Tree	0.47	0.19	0.0241
8	Fruit	Var. parc.	0.33	0.19	0.1015
9	Seeds	Visit. rate	0.01	0.2	0.9961
10	Seeds	Var. parc.	0.15	0.24	0.5456
11	Sugar	Visit. rate	0.27	0.19	0.1898
12	Sugar	Fruit	−0.11	0.19	0.5742
13	Sugar	Seeds	−0.08	0.2	0.6899
14	Weight	Visit. rate	0.04	0.17	0.807
15	Weight	Fruit	−0.39	0.16	0.0316
16	Weight	Seeds	−0.39	0.17	0.0402
17	Weight	Qual. Col.	0.48	0.19	0.0376

between cultivars (Sapir et al., 2017).

In our system, all farms were conventionally managed, with frequent application of insecticides (neonicotinoids or organophosphates), which might explain the absence of wild bees (*e.g.* see Mallinger et al., 2015; Rundlöf et al., 2015), although further investigation regarding this issue is needed. The lack of any semi-natural habitats remaining in this intensively-managed valley can also be a factor preventing the occurrence of wild bees within the orchards (Potts et al., 2010; Garibaldi et al., 2016; Geslin et al., 2016). Therefore, several questions remain on the effect of pollinator friendly management practices (e.g. reduced pesticide use, creation of patches of native flowers) on pollination services through increased populations of wild bees.

5. Conclusion

Our study showed that easily implemented changes in the management of honey bee colonies rented for pollination can improve visitation rates and thereby the quantity and quality of apple production resulting in higher farmers' profits. Given that the demand for pollination services is increasing faster than the supply of honey bee colonies (Aizen and Harder 2009), our results suggest that honey bee management practices aimed at improving colony quality can help to overcome this potential deficit in colony numbers. This is especially important for fruit production in our study system, which represents the largest fruit producing areas of an important fruit exporting country like Argentina, where the pollination process relies uniquely on *A. mellifera*. Facing the observed decline in wild bees in many parts of the word, such a situation might unfortunately become widespread.

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