The economic cost of losing native pollinator species for orchard production

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Abstract

1. The alarming loss of pollinator diversity worldwide can reduce the productivity of pollinator-dependent crops, entailing potential economic impacts. However, it is unclear to what extent the loss of a key native pollinator species affects crop production and farmer's profits.

2. By experimentally manipulating the presence of colonies of honey bees and a native bumble bee species (*Bombus pauloensis*) in eight apple orchards in South Argentina, we evaluate the impact of losing natural populations of a key native pollinator group on *i*) crop yield, *ii*) pollination quality, and *iii*) farmer's profit. To do so, we performed a factorial experiment of pollinator exclusion (yes/no) and hand pollination (yes/no).

3. Our results showed that biotic pollination increased ripe fruit-set by 13 % when compared to non-biotic pollination. Additionally, fruit-set and the number of fruits per apple tree was reduced by less than a half in those orchards where bumble bees were absent, even when honey bees were present at high densities. Consequently, farmer's profit was 2.4-fold lower in farms lacking bumble bees than in farms hosting both pollinator species. The pollination experiment further suggested that the benefits of bumble bees could be mediated by improved pollen quality rather than quantity.

4. *Synthesis and applications*: Our findings highlight the pervasive consequences of losing key pollinator functional groups, such as bumble bees, for apple production and local economies. Adopting pollinator-friendly practices such as minimizing the use of synthetic inputs or restoring/maintaining semi-natural habitats at farm and landscape scales, will have the double advantage of promoting biodiversity conservation, and increasing crop productivity and profitability for local farmers. Yet because the implementation of these practices can take time to deliver results, the management of native pollinator species can be a provisional complementary strategy to increase economic profitability of apple growers in the short term.

1. Introduction

Animal pollinators play a key role in agroecosystems, contributing to increased yield of most crops worldwide (Klein et al., 2007; Aizen, Garibaldi, Cunningham, & Klein, 2009). Yet, intensification of farming practices threatens pollinator and pollination services (Potts et al., 2010, 2016a) at the same time that demand on pollinator-dependent crops grows continuously (Aizen & Harder, 2009). Habitat loss, landscape fragmentation and overuse of agrochemicals are all important drivers of pollinator decline in agricultural landscapes, along with the introduction of exotic species and pathogens (González-Varo et al., 2013; Vanbergen et al., 2013; Goulson, Nicholls, Botías, & Rotheray, 2015). Given the importance of pollinators on food production, decrease of pollination services might generate scenarios of scarcity, or low diversity of food (Potts et al., 2016b). Therefore, a transition to more sustainable production systems, and a better understanding of the role of managed and wild pollinators for food production must be prioritized (Garibaldi, Requier, Rollin, & Andersson, 2017).

A wide diversity of wild bee species are recognized as highly efficient pollinators for crops (Garibaldi et al., 2011, 2013; but see Rader et al., 2016). Among the latter, large-sized species such as bumble bees (Apoidea) are disproportionally efficient as pollinators of both wild and cultivated plant species (e.g. Javorek et al., 2002). These large-sized species are also more sensitive to environmental changes and intensive farming practices (Rundlöf et al., 2015). Bumble bees in particular have suffered a general decline worldwide (Bommarco, Lundin, Smith, & Rundlof, 2012; Arbetman, Gleiser, Morales, Williams, & Aizen, 2017). In Latin America (LA), wild bee diversity, including several species of native bumble bees (e.g. *Bombus dahlbomii,* Guérin-Méneville, 1835; *B. pauloensis,* Friese, 1913), has declined dramatically, especially with the introduction of the European bumble bees *B. terrestris* (Linnaeus, 1978) and *B. ruderatus* (Fabricius, 1775) (Morales, Arbetman, Cameron, & Aizen, 2013), the use of agrochemicals and the transformation of landscapes by intensive agriculture expansion (e.g. Breno et al., 2009; Martins & Melo, 2010).

To satisfy the pollination demand in absence of native bumble bees and other wild pollinators that provide efficient and sustainable crop pollination services, farmers routinely practice massive supplementations of managed pollinator such as the Western honey bee (*Apis mellifera* L.*)* (Goodwin, Cox, Taylor, Evans, & McBrydie, 2011; Aebi et al., 2012; Rucker, Thurman, & Burgett, 2012; Geslin et al., 2017). However, this practice might not optimize crop yield as high densities of honey bees at the farm level can result in undesirable outcomes (Rollin & Garibaldi, 2019). For example, high visit frequency, that may result from an oversupply of managed bees or from extremely high abundances reached by invasive species, can limit crop production as a result of increased flower style damage (e.g., Sáez, Morales, Ramos, & Aizen, 2014) or stagnated pollen-tube populations resulting from scramble competition for style resources (e.g. Harder, Aizen, & Richards, 2016). Moreover, because honey bees are not necessarily efficient pollinators of some crops or crop production may depend on different pollinator species, it is not expected that honey bees by themselves are able to maximize crop yield (Garibaldi et al., 2013, 2016; Grass et al., 2018; MacInnis & Forrest, 2019).

Apple (*Malus domestica,* Rosaceae) is a high value, pollinator-dependent crop (great dependence according to Klein et al., 2007) as it is highly self-incompatible and requires cross-pollination between different cultivars to increase crop yield (Modlibowska, 1945; Ramírez & Davenport, 2013). Several wild bees, including native bumble bees (*Bombus* spp.) and solitary bees (e.g. *Osmia* sp.), as well as hoverflies have been described as efficient pollinators of apples (Földesi et al., 2016; Ramírez & Davenport, 2013). Argentina is one of the 15 main apple producers and exporters in the world, and therefore, this crop represents an important source of economic income (FAO, 2018). Yet, typical commercial Argentinian apple orchards are characterized by a low abundance of wild pollinators, probably due to intensive crop management and use of pesticides (Geslin et al., 2017). For example, a previous study reported a complete absence of wild visitors in several orchards

located in Neuquén Province, one of the most productive areas of the country (Geslin et al., 2017). One of the missing species is the black bumble bee (*Bombus pauloensis*)(sin. *Bombus atratus*; Sasal, 2016). This native species is widespread in South America, including the apple region of Neuquén as part of its historical southern range (Abrahamovich, Díaz, & Lucia, 2007). This bumble bee species has been identified as an efficient pollinator of different crops such as tomatoes, strawberries and peppers amongst others (Aldana, Cure, Almanza, Vecil, & Rodríguez, 2007; Riaño J., Pacateque E., Cure, & Rodríguez, 2016; Poveda-Coronel, Riaño J., Aguilar Benavides, & Cure, 2018), and has been reported as a floral visitor in apples (Abrahamovich, Tellería, & Díaz, 2001). Where many studies have focused on the relationship between honey bee density or pollinator diversity and crop production (Garibaldi et al., 2013, 2016; Sáez et al., 2014; Geslin et al., 2017; MacInnis & Forrest, 2019), only a few have assessed the individual contribution of key native pollinator species in crop production. Furthermore, as far as we know, no study has evaluated the effect on production and economic cost for local farmers of losing a particular pollinator species such as the black bumble bee.

We assessed the potential impact of losing the native black bumble bee by experimentally manipulating the presence of bumble bee colonies and managed honey bee hives in apple orchards on *i*) crop yield *ii*) quantity and quality of pollen deposition, and *iii*) economic outcome of Argentinean farmers. Given that bumble bees are efficient pollinators, and, functionally speaking, potentially complementary to honey bees, we hypothesize an increased crop yield and economic profit in farms hosting both colonies of bumble bees and honey bees.

2. Material and Methods

2.1. Study sites and experimental design

The experiment was carried out in the Alto Valle (Neuquén Province, Argentina), a region that produces most of the country's apples (85 %) (Geslin et al., 2017). We performed the pollination experiment from 16-24 September in 2016, which was the approximate bloom period for Red Delicious in this year.. We focused on Red Delicious, the most representative apple variety cultivated in this region. This variety is mostly self-incompatible, thus relying entirely on animal pollinators for compatible pollen transfer between trees (Geslin et al., 2017).

The experimental design consisted of eight conventional apple orchards separated by at least one km from each other and extending over a distance of 20 km along the main road in the valley (centroid located at 38°35'09.6"S 68°21'57.6"W) (see details in Geslin et al., 2017). We selected orchard with very similar abiotic (e.g., temperature, precipitation, soil characteristics, etc.) and biotic conditions (e.g., size and age of individual apple trees) in order to avoid potential confounding effects. The extremely low abundance of wild pollinators in apple orchards of the region (Geslin et al., 2017) allowed us to experimentally manipulate the abundance and composition of the bee assemblages. To do so, we placed honey bee hives in each experimental farm with a density of 7 hives per hectare, the recommended density in the Alto Valle Valle for apple pollination (Geslin et al 2017). A total of 24 colonies of black bumble bees (*B. pauloensis*) were placed in half of the experimental farms with six colonies per orchard (mean = 7 colonies per hectare) and approximately 80 workers per colony. They were provided by an Argentinian company that started breeding this species in captivity recently. The original idea of the study was to simulate realistic scenarios that are common among apple growers. In this sense, the introduction of honeybee colonies is a standard management practice, which is implemented by default by apple producers. Therefore, we decided to use this situation as our baseline scenario and avoid the scenario with bumble bees alone. In each orchard, we selected 1-ha plots and both honey bee hives and bumble bee colonies were deployed along one edge of the plots. Apple trees are planted in rows with the same

variety (Red Delicious), which are interdispersed with rows of the pollen-donor variety. We chose five trees per plot from which to collect data (detailed below), which were located approximately 3 m apart along a row that was located at least 15 m from the border of each plot. Individual trees were very similar in terms of height (approx. 4 m) and crop volume.

2.2. Pollination treatments and visits

On each focal tree, we applied four different pollination treatments following a two-by-two factorial design: *i*) flowers exposed to insect pollination (*IP*); *ii*) flowers exposed to insect pollination and supplemented with pollen manually *(IPS)*; *iii*) flowers excluded from all insects (*IE*), including potential wild pollinators; and *iv)* flowers excluded from insects but supplemented with pollen manually (IES). In the "no pollen-supplemented" treatments (*IP*, *IE*), tagged flowers were either freely exposed to insects (*IP*) or excluded with a 2 mm sized mesh bag (*IE*) with no further manipulation. In the hand-pollinated treatments (*IPS*, *IES*), we applied pollen manually from the appropriate pollen donor variety of the same crop using a paint-brush on receptive stigmas of fully open flowers. We applied pollen manually from Granny Smith, an appropriate compatible variety to pollinate Red-Delicious apple flowers. For each treatment, we marked 2-3 branches per tree with 4.2 ± 1.2 flowers/branch. Overall, we tagged a mean of 81 flowers (81± 20) per tree

Before blooming, we characterized the total flowering effort of each sampled tree. This was done by estimating the total number of buds per tree, which was calculated by averaging the number of buds for each of five branches and then multiplying this value for the number of branches of each individual tree. We monitored each orchard four times throughout the flower period and visited the orchard at different times of the day (from 0900h to 1900h). In order to estimate visit rates of both honey bees and bumble bees in crop flowers, we surveyed bees along four 100-m linear walks throughout each plot, which were separated 20-30 m from

each other. In order to standardize the sampling effort, each 100 m-walk was subdivided in three sections of one minute of observations with a constant walk speed (i.e. a total of 3 minutes for each 100 m-walk transect). Given the absence of wild pollinators in our experimental orchards (see also Geslin et al. 2017) and the high detectability of the two large-sized species, which are also easy to distinguish because of color and size differences, we firmly believe that this sampling design is appropriate to accurately estimate the abundance of visitors in apple flowers. In order to account for the potential effect of sun orientation and shadow area in the plot, we did side-focused observations with two of the walks surveying bees on the left, and two on the right side of the orchard row. The number of observed flower-visiting bees (i.e. the presence of a bee on a flower) was counted and identified as "honey bee" (*Apis mellifera*) or "bumble bee" (*Bombus pauloensis*). Overall, we conducted 108 100 m-walking transects during the whole season.

A chemical thinner was applied to apple trees at the end of the fruiting season to stimulate the dropping of misshapen fruits. It is important to note that thinning does not affect randomly all apples but selectively trigger the drop of worse-pollinated fruits. In addition, all orchards were conventionally managed, i.e., with intensive use of herbicides, fungicides, and insecticides (See Geslin et al. 2017 for more information) for avoiding potential damages of pests and pathogens on fruit production. In late February and early March, after chemical thinning and just before the harvest period, we counted the number of ripe fruits per tagged branches and estimated the ratio of ripe fruits to floral buds, hereafter (fruit-set), the number of fruits per tree, and collected fruits. Fruit weight was assessed during the following four days after harvest. We weighed each fruit ($n = 283$) to the 0.1 grams with an electronic scale to assign them to a price category (see below for details). Finally, we counted the number of developed seeds for all collected fruits.

2.3. Pollen deposition and pollen tubes

When the flowers were no longer receptive, we collected apple styles in 70% ethanol solution, and kept them for subsequent lab analyses. The styles were washed with distilled water and prepared with an aniline blue solution (Martin, 1959) in order to be observed under epifluorescence microscope. The number of pollen grains deposited on the stigmas and the number of pollen tubes that reached the bottom part of styles were counted for each treatment and tree ($n = 346$).

2.4. Statistical analysis

2.4.1. Flower-visiting bee abundance
Differences in abundance of honey bees and bumble bees visiting apple flowers were tested with a generalized linear mixed model (GLMM) with a negative binomial error structure. The abundance of flower-visiting insects per transect was modeled in response of the bee species (honey bee *vs.* bumble bee) with farm identity included as a random factor. Distributions of residuals were inspected to check the assumptions of the models.

2.4.2. Fruit-set, pollen deposition, growth of pollen tubes and seed development
For assessing differences in *i*) fruit-set, *ii*) number of pollen grains deposited in stigmas, *iii*) number of pollen tubes that grew along the style and, *iv*) number of developed seeds among pollination treatments and between farms hosting bumble bees and honey bees and farms hosting only honey bees we performed a set of GLMMs. The above-mentioned variables were used as responses whereas pollination treatment (*IP, IPS, IE, IES*) and the presence of bumble bees and its interaction were incorporated as fixed effects, and farm as a random effect. We used a Gaussian error structure for fruit-set, a *Poisson* error structure for the number of pollen grains and the number of pollen tubes, and a negative binomial for the number of developed seeds to account for overdispersion. Differences between different

levels of the fixed effects were evaluated with a posteriori multiple pairwise comparison (Tukey HSD test). Finally, we assessed the relationships between the number of developed seeds and pollen tubes in both types of farms by applying a GLMM with the number of seeds as response variable and the presence of bumble bees, the number of pollen tubes and its interaction as fixed effects, and the identity of the farm as a random factor. All analyses were performed with the glmmTMB (Brooks et al., 2017) and emmeans (Lenth, 2018) statistical packages in R (R Core Team, 2018).

2.4.3. Farmer's profit

We estimated the profit of farmers from apples in the two types of farms (with honey bees *vs.* with honey bees and bumble bees). Fruit price ranges according to three individual weight categories (*small:* <130 g; *medium:* 130 - 170 g; *large:* > 170 g). The prices were 0.38, 0.66 and 0.80 $USD· kg^{-1} for small, medium and large apples, respectively (Geslin et al., 2017). We estimated at the farm level the proportion of harvested fruits that belong to each of the three weight categories. The average costs associated with the farm inputs, excluding the price of honey bee and bumble bee colonies, was 0.28 $USD · kg^{-1} and approximately 80% of apple production was sold. All economic data was estimated by Geslin et al. (2017) for the same area in the previous year (2015), and thus, we used the same cost structure. Changes in market price between both years (previous and sampling year) are not expected to influence the conclusions of our results as we were interested in assessing the relative difference between both types of farms rather than absolute gains of farmers per hectare. Following a similar framework of that of Geslin et al. (2017), we estimated the farmer incomes as follow:

Apple profit: f · d · 0.8 (s·p·ws+m·p·wm+l·p·wl–(hcol·h+bcol·b)–f·d· 0.8 ·0.28 ·(s·ws+m·wm+l·wl)

where

f = number of fruits per tree

d = number of trees per hectare$s$

s = proportion of fruits in the small-sized category

p = price of small-, medium- or large-sized category

ws = mean weight of small-sized fruits

m = proportion of fruits in the medium-sized category

wm = mean weight of medium-sized fruits

l = proportion of fruits in the large-sized category

wl = mean weight of large-sized fruits

$hcol$ = number of honey bee colonies installed per hectare

h = rental price of a honey bee colony (20 US$ per colony)

$bcol$ = number of bumble bee colonies installed per hectare

b = acquisition price of a bumble bee colony (50 US$ per colony)

We tested the potential effect of the loss of bumble bees on the profit of farmers in apple orchards by applying a Wilcoxon non-parametric test to compare farms with and without bumblebees.

3. Results

The number of visits of honey bees per transect in apple flowers (mean ± SD, 61.7 ± 6.1) was almost two orders of magnitude higher (Z= 8.9, p< 0.05) than the visits of bumble bees (0.9 ± 0.3) in farms where bumble bees were introduced (Fig. 1). In farms where bumble bees were not introduced, only honey bees visited the apple flowers (57.1 ± 13.03) (Fig. 1). No statistical differences were found in the number of honey bees visiting apple flowers between both type of farms (Z=0.65, p> 0.05; Fig. 1).

Fruit-set in flowers that were exposed to insect pollination (*IP* and *IPS*) was more than two-fold higher in farms with bumble bees and honey bees than in farms hosting honey bees only (*IP*: t= -3.91, p< 0.01, *IPS*: t= -2.50, p< 0.01) (Fig. 2A). Flowers excluded from insect pollination (IE and IES) showed lower fruit-set than

flowers exposed to pollinators (IP and IPS) (see Fig. 2A for the rest of comparisons). Fruit-set in treatment *IPS* (insect access and pollen supplementation) was higher than in treatment *IES* (exclusion from insects and pollen supplementation), but only in farms where bumble bees were introduced ($t= 2.89$; $p= 0.07$).

Both the number of pollen grains deposited on stigmas and the number of pollen tubes that reached the bottom section of styles in flowers exposed to insect pollination (*IP* and *IPS*) in farms hosting bumble bees were not statistically different from farms that hosted only honey bees (Fig. 2B, Fig. 2C). Unexpectedly the number of pollen grains in the *IP* treatment (insect pollination, non-supplemented) was higher than in the *IPS* treatment (insect pollination, supplemented). As expected fruit-set, pollen deposition and pollen tubes in IE treatment (insect exclusion, non-supplemented) were lower ($p< 0.01$) than in the rest of treatments (Fig. 2). The number of pollen grains was positively associated to the number of pollen tubes that reached the bottom of the styles ($Z= 2.05$, $p< 0.05$). Yet, this relationship was very similar in both types of farms ($Z= 1.01$, p> 0.05; Fig. 3A).

The number of developed seeds was higher in farms hosting bumble bees than in farms hosting only honey bees ($Z= 3.319$, $p< 0.05$, Fig. 3B). Additionally, the number of developed seeds showed a positive relationship with pollen tubes only in farms lacking bumble bees ($Z= 2.45$, $p< 0.05$, Fig. 3C). In this sense, the number of developed seeds in farms without bumble bees only reached the values of farms with bumble bees in situations where the number of pollen tubes was high (Fig. 3C).

Number of fruits per tree and farmer profit (i.e. farmer income after deduction of production costs and colony rentals) was 4-fold and 2.4-fold lower ($W= 14$, $p< 0.05$) in farms lacking the native bumble bee species (Fig. 4), respectively. The average profit in these farms was 6774 ± 1533 $USD · Ha^{-1}, while farmers that installed colonies of both pollinator groups earned 16302 ± 5072 $USD · Ha^{-1} (Fig. 4B).

4. Discussion

Loss of key native pollinator species may not only have negative consequences on ecosystem functionality, but also on crop production (Potts et al., 2010). Here we demonstrate that fruit-set of apple farmers is reduced in the absence of native bumble bees. Interestingly, bumble bees did not increase pollen deposition and the formation of pollen tubes beyond that observed for honey bees alone. However, the higher success of pollination in terms of seed development observed in flowers exposed to bumble bee visitation suggests that benefits provided by this species might be mediated by changes in the quality of pollen they transfer (Aizen & Harder, 2007). Reduced fruit-set in apples translated to decreased crop yields, causing an important reduction in the farmer's economic benefits.

The exclusion of apple flower visitors reduced fruit-set drastically (Fig. 2A), which confirms that apple is highly dependent on animal-mediated pollination (Klein et al., 2007). The most common management practice used to increase yield of pollinator-dependent crops consists in adding high amounts of honey bees (Goodwin et al., 2011; Aebi et al., 2012; Rucker et al., 2012). However, recent evidence shows that honey bees, even when present at high abundances, are not able to close yield gaps when other wild pollinators that complement crop pollination are not present (Garibaldi et al., 2013; MacInnis & Forrest, 2019). Fruit-set of apples was reduced by more than half in farms with high densities of honey bees but lacking native bumble bees compared to farms with both pollinator groups. These differences are not attributable to differences in honey bee visitation rates between the two types of farms as density of beehives introduced was the same and the abundance of foraging honey bees was quite similar. In addition, flowers that were excluded from pollinators after being supplemented manually with pollen (treatment IES) showed a 5% lower fruit-set compared to those that were supplemented and exposed to insect pollination (treatment IPS). Interestingly, this pattern only occurred in farms where

both honey bees and bumble bees were present, suggesting that pollen and/or flower handling by bumble bees has an important positive effect on fruit-set. We have to interpret this last result with caution as the *p-value* associated to the statistical model was just marginally significant ($p = 0.07$).

The increased fruit-set in apples on farms with bumble bees cannot be attributed to an increase of pollen grains received by stigmas, or in the number of pollen tubes that reached the bottom of the style. Pollen deposition and tubes growth showed high variability, and no statistical differences were found between farms hosting both pollinator species and farms hosting only honey bees. Therefore, the most parsimonious explanation to the differences in fruit-set could be attributed to differences in the quality of pollen transferred by the two species. In this sense, the number of developed seeds was low in farms where the bumble bees were absent. Apples showed a high number of developed seeds (i.e., similar to apples harvested in farms with bumble bees) only when the number of pollen tubes increased considerably (see Fig. 3C). This suggests that each single pollen grain deposited (and pollen tube growing) in bumble bee-exposed flowers has a higher probability of fertilizing an ovule and bearing a seed than pollen grains deposited in flowers exposed only to honey bees.

Foraging behavior of both species could account for these differences. Honey bees usually move between trees less frequently and over shorter distances than bumble bees (Dupont, Hansen, Valido, & Olesen, 2004; McBrydie, Howlett, & Pattemore, 2017; but see Palmer-Jones & Clinch, 1966; Miñarro & García, 2018), thus, promoting geitonogamy (i.e. pollen transfer among flowers of the same individual). This is expected to reduce outcrossing (e.g. Whelan, Ayre, & Beynon, 2009), activating late-acting pre-zygotic or post-zygotic barriers that reject self pollen (Seavey & Bawa, 1986), even when pollen deposition is high. Several studies performed in both natural and agricultural ecosystems have also found a low

production of seeds in contexts where honey bee density is very high and dominates the assemblage of pollinators (Rollin & Garibaldi, 2019; Valido, Rodríguez-Rodríguez, & Jordano, 2019).

Insect pollination has a high market value in apple production as suggested previously (Garratt et al., 2014; Geslin et al., 2017) and confirmed by our results. In our experimental farms, honey bee pollination provides an average net income of 6774 $USD/Ha^{-1} to apple farmers. This economic performance is unexpectedly lower than the values reported by Geslin et al. (2017) in the previous years, who found a mean profitability per hectare of 12,080 $USD/Ha^{-1}. Given that we used the same experimental farms, we expected a similar mean profitability in apple orchards as that reported by Geslin et al. (2017). Inter-annual differences in abiotic conditions and/or management practices could explain this result as these factors may modify potential crop yield across years (Lobell, Cassman, & Field, 2009). Yet we found that mean profitability in farms where bumble bees were additionally introduced was 30% higher (16302 $USD/Ha^{-1}) than those reported by Geslin et al. (2017). This result would highlight the importance of promoting insect diversity in productive landscapes, as the impact of climatologically unfavorable years on crop yield could be buffered by the presence of pollinators with different susceptibility to adverse climatic conditions. Differences in the quality of beehives introduced, which has been identified as a critical factor influencing crop yield (Geslin, et al., 2017), could also explain the pattern found. We hypothesized that biodiversity loss at farm scale would reduce crop productivity and economic profit of farmers (Garibaldi et al., 2013; Rader et al., 2016). Accordingly, we found that losing a single key species such as the native black bumble bee reduced the economic performance by more than half in apple orchards. Profits in farms hosting two pollinator groups are still slightly low when compared with more biodiverse apple farms (Garratt et al., 2014), suggesting that, by enhancing pollinator diversity, there is still room for increasing profitability in our depauperate farms.

5. Conclusions

Anthropogenic impacts are triggering unprecedented rates of wild pollinator declines (González-Varo et al., 2013; Vanbergen et al., 2013 ; Goulson et al., 2015) with negative consequences for ecosystem functioning and crop production (Potts et al., 2010). Our results show that crop yield and farmer's profit might be reduced drastically after the disappearance of a key functional group, even when abundance of managed honey bees is high. This emphasizes the importance of properly managing farms in order to meet the rising demand of food while conserving the full range of wild pollinator species. Adopting pollinator-friendly practices at farm and landscape scales (Garibaldi et al., 2019) will have the double advantage of promoting biodiversity conservation and increasing crop productivity and profitability. Yet because ecologically intensive practices can take time to deliver results (e.g. enhance pollinator diversity and abundance)(Garibaldi et al., 2019), the management of native pollinator species, such as in the Alto Valle, can be a provisional complementary strategy to increase economic profitability of apple growers in the short term.

Author contribution

All author conceived the idea and designed the study. GA, FR, JH and NG collected data. JH and GA performed lab analysis. NPM analyzed data with substantial inputs from LG, GA and MA, and wrote a first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accesibility

Data will be available via the Dryad Digital Repository

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Figures

Fig. 1. Abundance (bees · transect^{-1}) of honey bees (*Apis mellifera*, yellow boxes) and the native black bumble bees (*Bombus pauloensis*, grey boxes) visiting flowers in apple orchards at farms where colonies of bumble bees have been introduced (*Yes*) and farms where colonies of black bumble bees have not been introduced (*No*). Grey dots represent transects, boxes show the inter-quartile range (IQR), horizontal line represent the median, whiskers show the range of 1.5*IQR. Icons: www.freepik.com
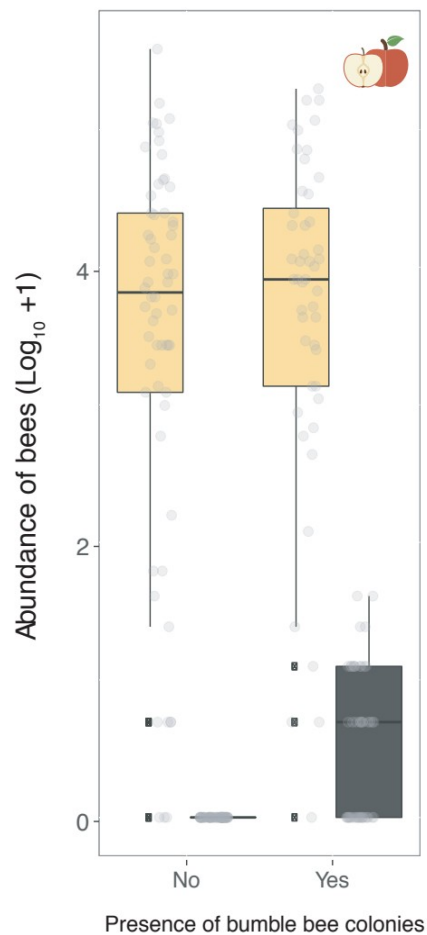
Fig. 2. Effects of pollination treatments (*IP, IPS, IE, IES*) on ripe fruit-set (Panel A), pollen deposition (Panel B), and growth of pollen tubes (Panel C) (mean ± SE) on farms hosting honey bees (*Apis mellifera*) and the native black bumble bees (*Bombus pauloensis*, grey bars) and farms hosting only honey bees (yellow bars). Same letters indicate no statistical differences between treatments. Asterisks (*) Indicate marginal statistical differences between treatments (p = 0.07). Icons: www.freepik.com
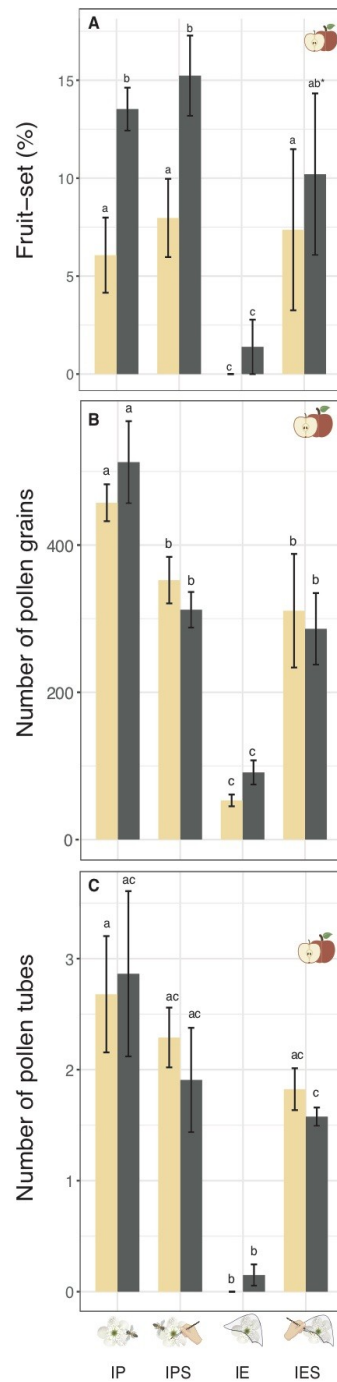
Fig. 3. Panel A: Relationship between the number of pollen grains deposited and the number of pollen tubes that reached the bottom section of the style of apple flowers in orchards hosting honey bees (*Apis mellifera*) and the native black bumble bees (*Bombus pauloensis*, grey) and orchards hosting only honey bees (yellow). Panel B: Number of developed seeds of apples from flowers exposed to pollinators (IP treatment) in both types of apple orchards. Panel C: Relationship between the number of pollen tubes that reached the bottom section of the style and the number of developed seeds in both types of apple orchards. Icons: www.freepik.com
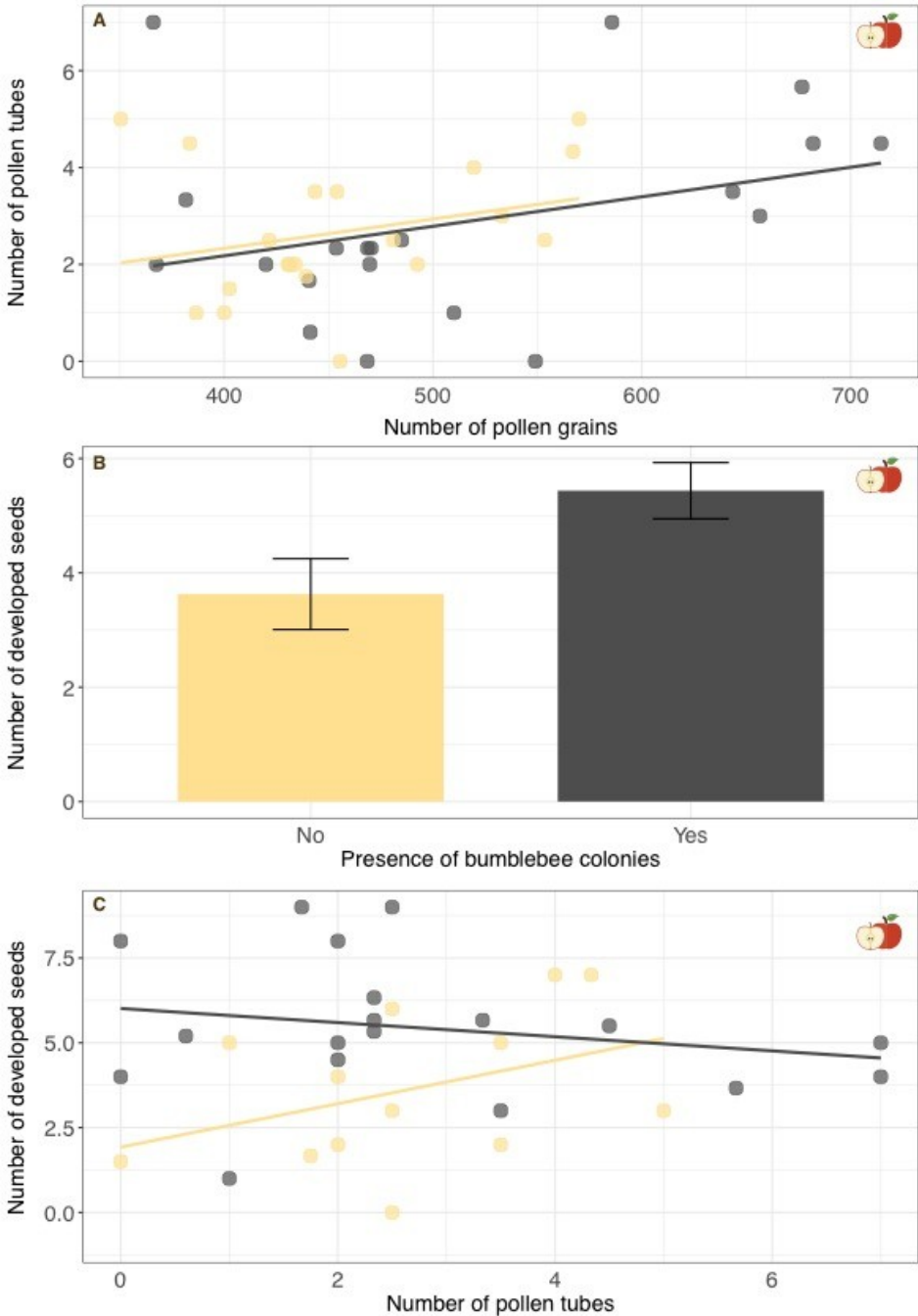
Fig. 4. Number of fruits per tree (panel A) and farmer's net income in $USD per hectare (mean ± SE) (panel B) in apple orchards where colonies of bumble bees have been introduced (*Yes, grey bars*) and farms where colonies have not been introduced (*No, yellow bars*). Icons: www.freepik.com