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Hived native Cape honey bees provide a reliable and inexpensive pollination service for high-quality apple production in the Cape Floristic Region

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Abstract

Pollination ecosystem service studies across multiple crops in many countries have shown that managed pollinators often complement wild pollinators. Such studies typically compare farms with or without access to wild pollinators, without controlling for the introduction of honey bee hives. Here, we compared three pollination strategies in commercial apple orchards in the Cape Floristic Region (CFR) of South Africa: (i) orchards relying exclusively on managed pollination through the introduction of hives of the endemic Cape honey bee (*Apis mellifera capensis*); (ii) orchards relying solely on pollination from all wild indigenous pollinators, including the Cape honey bee; and (iii) orchards using a combination of both sources. We found that pollination across all three pollination options was almost entirely from the Cape honey bee, but with significantly fewer flower visits in wild orchards. Wild pollinated orchards produced significantly fewer seeds per apple compared to orchards with hived honey bees, resulting in fewer apples of marketable size or shape. Hived bees resulted in the highest proportion of high-quality fruit. Summed across all farms, excluding insect pollination led to a ~95% reduction in the number of apples per tree, while in terms of apple marketability, failure to rent hives at 2 hives per hectare resulted in a 17.4-percentage-point reduction in high-quality fruit. Use of hived native honey bees in the CFR should therefore be considered an essential management input and an insurance measure for maintaining high-quality apple production. Our study emphasizes why local context should take precedence over broad international policy recommendations for optimal management of pollination services.

Keywords: Agroecosystem; Fruit set; Native honey bees; *Apis mellifera capensis*; Landscape context; Apple production; South Africa

1. Introduction

Several studies quantify the ecosystem services that wild pollinators provide to crops dependent on insect pollination.[1-7] These studies indicate that crops grown near natural or semi-natural areas are readily pollinated by wild insects, which provide essential insurance against possible shortages in the supply of managed bees[8] or, alternatively, stabilize the pollination service received due to functional complementarity.[9,10] Notwithstanding these efforts over the last decade and a half, one managed pollinator species, *Apis mellifera*, remains the most important pollinator species in global agriculture.[4,9,11] To date, few practical methods are available for using wild bees in most commercial crops that require pollination in agriculturally intensive settings,[12-14] and this is likely to remain the case for the foreseeable future.[15,16]

Only a few studies compare the pollination service of managed honey bees with that of wild pollinators (e.g., Klein *et al.*[4]). Some studies assume honey bees are managed when comparing them to wild pollinators,[6,7] while other studies focus on crop systems adjacent to natural areas and compare pollination efficiency of wild pollinators in terms of honey bee density.[6,7,10] An alternative approach is to compare orchards that do or do not use managed honey bees but have access to wild pollinators, and then relate this to fruit set and yield.[17] Some studies do compare flower visitation and efficiency between wild pollinators and managed honey bees[10,17,18] but find it difficult to separate wild and managed pollination service within the same commercial crop—a choice often faced by the growers. In fact, the type of pollination service used will depend on the cost versus benefit realized by the grower of a pollinator-dependent crop.[19] This highlights the need to compare the economic ramifications of different pollination service options.

The fundamental issue is to compare the relative efficiency and quality of pollination ecosystem services provided by wild pollinators to the managed pollination service rented by commercial growers, when these options are available under comparable farm conditions. If these services do not differ significantly, growers can save costs by not hiring managed honey bees for pollination when their crops are close to natural vegetation[1,4] and may have gained "pollination insurance" against managed honey bee losses.[8] The converse also applies: managed honey bees can be used as a safety net when native honey bees (or other bee species) are being relied upon in natural areas. This concern arises from factors such as adverse weather (e.g., severe drought), the magnet effect of large displays of indigenous vegetation drawing bees away from orchards,[20] and/or long distances between wild nests and the crop being pollinated.[21] The first two factors may be particularly significant in the Cape Floristic Region (CFR) biodiversity hotspot, which is characterized by high drought and fire risk.

Apple production is a cornerstone of the thriving deciduous fruit industry in the CFR; consequently, we used apple orchards to compare the services provided by wild and managed pollinators in this region. In this geographical region, most apple orchards in the CFR employ native-managed honey bees (the endemic Cape honey bee, *Apis mellifera capensis*), stocked at two hives per hectare as per industry standard.[22] The associated costs are only about 1% of total production costs,[22,23] which is an important consideration. Owing to the CFR's mountainous terrain, many orchards border natural vegetation. These areas are often extensive, relatively undisturbed, and support a high diversity of wild pollinators.[24] This suggests that apple orchards adjacent to natural areas should benefit from access to a wild pollination service (sensu Kremen *et al.*[1]) in addition to the rented hives (i.e., having a mix of managed and wild pollinators). Three pollination strategies are therefore distinguishable: (i) exclusively managed (hived) pollination, (ii) exclusively wild pollination, or (iii) a mix of wild and managed pollination.

Our hypothesis is that managed and wild pollination regimes are comparable in terms of the efficiency and quality of pollination services, but that the mixed strategy is superior due to synergistic effects between wild and managed pollinators.[6,7]

2. Methods

2.1. Study area and site selection

Our study area comprised apple orchards located in the Ceres and Witzenberg valleys (33°09' to 33°24' S and 19°13' to 19°35' E) and the Elgin, Grabouw, and Villiersdorp area (33°58' to 34°15' S and 19°00' to 19°20' E), two of the major deciduous fruit producing regions in the Western Cape of South Africa (Figure A1). The predominant natural vegetation in the study area is sclerophyllous fynbos, a Mediterranean-type vegetation characteristic of the CFR.[25] Of the commercially grown apple cultivars in the region, "Granny Smith" was chosen as the study cultivar, as it benefits from cross pollination[26] and is the most extensively produced cultivar in South Africa (in 2008, comprising 25% [i.e., 5,050 hectares] of all apple orchards.[23])

Twelve individually managed "Granny Smith" orchards (>2.5 km apart) were selected as study sites, first based on the potential for wild pollinators to access the orchards (far from versus close to semi-natural or natural vegetation), and second, on whether these orchards received hived honey bees. This resulted in three pollination sources: (i) four orchards relying only on managed pollination through hive introduction of the native Cape honey bee, (ii) four relying only on wild pollination, potentially from all local pollinators, and (iii) four using both pollination sources (wild and managed). All orchards were conventionally managed and subject to management practices that promote flowering followed by fruit thinning.[23,27] We were able to select only four farms that relied solely on wild pollinators, as most growers had already opted to introduce hived bees.

Orchards were selected by using 1:50 000 maps (Chief Directorate: National Geo-Spatial Information, Private Bag X10, Mowbray, South Africa) and Google Earth, and were verified by on-farm inspection to confirm the use of managed honey bees during the pollination season and the presence of good quality natural habitat (e.g., areas that had not recently burned, a regular natural occurrence in the area). We observed a major difference between the landscapes sampled: some orchards were >2 km from large patches of natural vegetation, while others were < 1 km from such patches. Two kilometers was taken as the minimum distance for denoting orchards as far from wild or managed pollinators. While this distance may not exclude larger bee species, Blitzer *et al.*[10] used a distance of 1.9 km to ensure independence in forager visits between orchards (Zurbuchen *et al.*[28]). In addition, Carvalheiro *et al.*[29] found that *Apis mellifera scutellata* densities start to decrease at distances > 1 km from natural edges in large sunflower fields. Thus, although honey bees can fly much farther, most foraging visits occur within < 1 km.[30]

The features of the landscapes surrounding these apple orchards (landscape metrics sensu Blitzer *et al.*[10] and Eeraerts *et al.*[31]) were quantified using the most recent South African land-cover data to specify land-use type (derived from the 2013–2014 South African National Land-Cover Dataset, with a resolution of 30 m × 30 m cells equivalent to the Landsat 8 multispectral imagery).[32] Buffers with radii of 1 km and 2 km were placed around each selected apple orchard, and the surrounding landscape was classified as shown in Figure A1. Landscape metrics included: (i) the percentage of natural or semi-natural vegetation, (ii) the total percentage of agricultural land, (iii) the area of natural vegetation, and (iv) the ratio of natural vegetation to crop area.

Orchards relying solely on wild pollinators did not differ significantly from those using both pollinator sources in any landscape metrics. In contrast, orchards classified as relying solely on managed pollination had a lower percentage of semi-natural and natural vegetation and a greater percentage of crop area. These sites also contained fewer hectares of continuous natural vegetation, and smaller natural-to-crop-area ratios (Table 1). This indicates the presence of less suitable potential habitat and overall landscape conditions for wild pollinators around these orchards.[31]

2.2. Sources of insect pollinators

The natural vegetation in the CFR biodiversity hotspot is rich in insect pollinators, including many species of solitary bees, carpenter bees, syrphid flies, monkey beetles, and butterflies.[20,24,33,34] Of particular significance is that the CFR is also home to *Apis mellifera capensis*, which, in addition to being indigenous, is an important generalist pollinator for many flowering plant species.[33,35,36] The managed honey bees used for pollination in this region are also *Apis mellifera capensis*, with beekeepers typically trapping wild swarms to replenish lost colonies.[36,37] It is one of the few areas in the world where wild and managed honey bee colonies are not only of the same species but also co-occur. The major difference between wild and managed honey bees is that wild colonies are resident and linked to local flower availability, whereas managed honey bees are imported into orchards and their densities are independent of local flower availability.[38] Consequently, the colony strength of wild colonies in spring is likely to be lower than that of managed colonies because beekeepers actively manage colony strength leading up to crop pollination. We therefore expect wild honey bee individuals to track annual flower resource availability, as do other resident wild non-*Apis* pollinators worldwide, and to differ from managed honey bees (despite being the same subspecies).

2.3. Exclusion experiment setup

In each of the 12 study orchards, 25 trees were selected (five adjacent trees per row in five rows randomly selected throughout the orchard). For insect exclusion, one branch per tree was enclosed in a 35 cm × 50 cm mesh bag with a 2 mm mesh size, allowing sufficient air flow and wind pollination while excluding insect pollination. A branch with the same characteristics as the bagged branch was marked and used as an open control.[39] The experimental and control branches each had ≥ 3 flower clusters and were located at least > 1 m from the tree trunk to ensure sufficient sunlight for maximum flower productivity. Similar to Mallinger and Gratton,[17] mesh bags were installed immediately before flowering and removed one month later, when all flower petals had fallen, to allow similar conditions for fruit development compared with open branches. This ensured the validity of comparing the fruit production between control and enclosed branches within each apple tree.

Table 1. Landscape characteristics of areas surrounding selected apple orchards for the experimental evaluation of pollination service options on production quantity and quality

Quantified landscape variable	Measure	Orchards using managed pollination	Orchards using both types of pollination	Orchards using only wild pollination
% natural land within a 1 km radius	Min	21.8	42.6	53.2
	Mean	27.7	55.4	59.8
	Max	37.8	69.4	67.2
% crop land within a 1 km radius	Min	60.4	21.7	32.1
	Mean	68.1	37.7	35.5
	Max	75.4	52.8	39.8
Hectares of natural vegetation within a 2 km radius	Min	70.5	412.4	378.2
	Mean	159.3	541.6	534.0
	Max	258.9	755.2	641.8
Ratio of natural to crop within a 2 km radius	Min	0.3	1.2	1.4
	Mean	0.5	2.5	1.9
	Max	0.6	3.5	3.1

2.4. Sampling insect flower visitors

Flower visitor abundance in each orchard was determined by the same observer counting all flower-visiting insects making contact with the reproductive parts of flowers, as observed within 1 min on one side of a tree. This seemingly short time period is adequate for recording easily visible pollinator individuals against the white background of the flowers. This procedure was repeated on six adjacent trees in five rows (adjacent to those used for the exclusion experiment), resulting in a total sampling effort of 30 trees for 30 min per orchard.

Surveys were all conducted when orchards were at 50% full bloom on clear, sunny days (following Carvalheiro *et al.*[29]), between 09:00 and 12:00, with a temperature > 18 °C, and wind speeds < 15 km hr^{-1}. Environmental variables, including wind speed, temperature, relative humidity, time of day, and percentage cloud cover, were used as independent variables to explain flower visitation.

2.5. Measuring pollination success

Pollination does not necessarily translate into adequate fruit production,[40] so here we tracked both the quality and quantity of pollination service through to final fruit production. The number of fruitlets formed per branch on all 25 sampled trees per orchard was first counted after pollination and flower drop (when exclusion bags were removed), and again shortly before harvest (following Blitzer *et al.*[10]). This allowed the initial number of fruitlets produced and the final number of fruit available for harvest to be recorded,[41] in addition to the number of flowers per branch. These data were used to calculate the initial and final fruit set.

2.6. Sampling fruit and assessing quality

A maximum of 30 fruit per orchard (with a maximum of five fruit per marked branch) were collected five days before harvest for laboratory analyses of seed set and fruit quality. Measurements included weight (g), diameter (mm), and shape. Apples were then cut open to count the number of fully formed seeds per fruit. Apple shape was visually assessed by the same observer: fruit with an evenly round shape was classified as normal, whereas skewed or lopsided fruit was classified as malformed. Fruit quality, and thus marketability, was represented by two variables: fruit of standard size (industry minimum for individual apple: weight ≥ 90 g and diameter ≥ 60 mm) and fruit of standard shape (i.e., not malformed or lopsided).

2.7. Data analyses

To address whether orchards using different pollination sources varied in the number of flower visitors observed, pollination performance, and quality of harvested fruit (i.e., all variables listed in Figure 1), responses were compared between open and closed branches during the flowering period using mixed-effects models. Farm identity was included as a random effect in all models to account for between-farm differences and spatial location. For the model analyzing the number of flower visitors, row nested within farm was included as an additional random effect. Fixed effects included pollination source (managed versus both versus wild), branch treatment (open versus closed), and the pollination source × branch treatment combination (managed–open versus managed–closed versus both–open versus both–closed versus wild–open versus wild–closed), all treated as categorical variables.

Additionally, biotic variables (number of flowers or number of seeds) or abiotic variables (wind speed, temperature, relative humidity, time of day, and percentage cloud cover) were included as fixed effects as appropriate for the dependent variable. Mixed model selection was performed by fitting all combinations of fixed effects for each response variable and ranking models according to the lowest Akaike information criterion (AIC) or the lowest number of variables in the model if ΔAIC < 1. Generalized linear mixed-effects models (GLMMs) were used for all dependent variables that did not follow a normal distribution, except for fruit weight, which was normally distributed and therefore analyzed using a linear mixed-effects model (LMM). When an LMM was used, the nlme *R* package was applied, whereas the lme4 *R* package was used for a GLMM.[42]

3. Results

3.1. Flower visitor abundance during sampling window

Counts of flower visitors recorded a total of 587 honey bee flower visits (or an average of 1.78 honey bees per minute of observation). Apart from honey bees, only seven individuals of other insect visitors were recorded across all observed flowers (one *Lepidoptera* sp., one hymenopteran *Xylocopa* sp. [Apidae], four Syrphidae, one *Coleoptera* sp.). Flower visitor counts thus showed that 98.8% of the recorded apple flower visitors were the indigenous honey bee (*Apis mellifera capensis*).

Orchards using managed pollination were not significantly different from orchards using both pollination sources in the median number of honey bees observed min^{-1} tree^{-1} (Figure 1A; Table 2). In contrast, orchards relying exclusively on wild pollination had significantly fewer honey bees (Table 2), with a median of zero visits (Figure 1A). In addition, wind speed (range 0–10 km h^{-1}; mean 2 km h^{-1}) had a significant negative effect on the number of honey bees recorded; however, due to the small slope estimate, this effect was of lesser importance compared to pollination source (Table 2).

3.2. Pollination success and fruit quality

Model selection indicated that mixed models of all pollination success and fruit quality dependent variables performed better when the pollination source × branch treatment combination was included as an explanatory variable, except for fruit size and fruit shape (Table A1).

The number of flowers per branch differed significantly among the three pollination systems. Wild-pollinated orchards had fewer flowers, while open, managed pollinated orchards had significantly more flowers than any other pollination system–treatment combination (Figure 1B; Table 2). Orchards using different pollination systems did not differ significantly in initial or final fruit set, although there was a general difference between open and closed branches (Figure 1C and 1D; Table 2). The number of seeds per apple in orchards using both pollination services did not differ significantly from orchards relying solely on managed pollination, whereas orchards using only wild pollination had significantly fewer seeds (Figure 1E; Table 2).

Of the 1,340 fruit produced on all marked branches, 612 (approximately 45%) were harvested and processed in the laboratory (409 from open branches and 203 from closed branches). Fruits with more seeds were significantly more likely to be of standard size and of standard shape (Table 2; Figure 2A and 2B).

The four pollination treatments applied to marked branches—managed pollination only, mixed pollination, wild pollination only, and insect pollinators excluded—resulted in different numbers of apples sold fresh or processed prior to sale. Processed apples were smaller and had fewer seeds than fresh apples (Table A2).

3.3. Extrapolated financial implications

Apples are sold either as fresh fruit (local and export markets) or as processed products (concentrate for various products). We used 2024 seasonal prices[23] to estimate differences among the three experimental scenarios. Although extrapolating branch-level exclusion

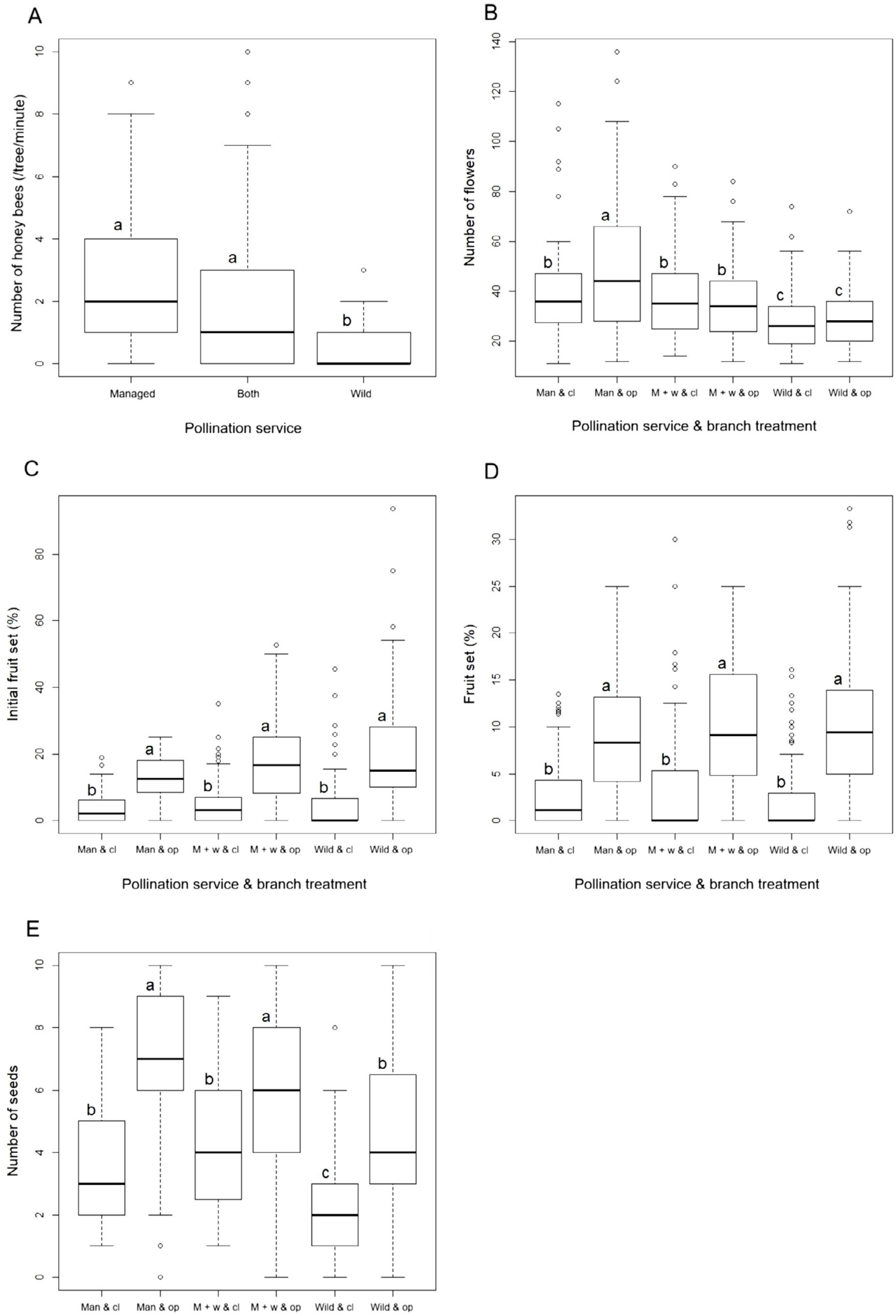

Figure 1. Pollination-success variables and fruit quality variables were compared among pollination-service categories (managed, managed + wild, and wild pollination) and branch treatment (closed, open) combinations used in the sampled orchards with respect to: (A) number of honey bee foragers counted per tree in one minute; (B) number of flowers per branch; (C) initial fruit set; (D) final fruit set; and (E) number of seeds per apple. Different letters (a, b, and c) indicate significant differences between groups at $p < 0.05$ (Table 2). Cl denotes closed; man denotes managed; op denotes open; w denotes wild.

Table 2. Best-fitting mixed models explaining honey bee flower visitation, pollination success, and fruit-quality variables

Dependent variable	Model parameters		
	Factor	Slope estimate (± SE)	*z*-value
Number of honeybees	Managed + wild	−0.279 ± 0.547	−0.51
	Wild	−1.723 ± 0.618	−2.79**
	Wind	−0.070 ± 0.034	−2.05*
Initial fruit set	Managed and closed	0.000 ± 0.000	–
	Managed and open	1.466 ± 0.097	15.03***
	Managed + wild and closed	0.213 ± 0.348	0.61
	Managed + wild and open	1.546 ± 0.343	4.50***
	Wild and closed	−0.130 ± 0.355	−0.37
	Wild and open	1.800 ± 0.344	5.24***
Final fruit set	Managed and open	1.205 ± 0.117	10.34***
	Managed + wild and closed	0.082 ± 0.311	0.26
	Managed + wild and open	1.230 ± 0.303	4.07***
	Wild and closed	−0.516 ± 0.331	−1.56
	Wild and open	1.257 ± 0.306	4.11***
	Flowers	−0.004 ± 0.002	−2.35*
Number of seeds	Managed and open	0.733 ± 0.077	9.48***
	Managed + wild and closed	0.222 ± 0.161	1.38
	Managed + wild and open	0.522 ± 0.152	3.43***
	Wild and closed	−0.713 ± 0.185	−3.85***
	Wild and open	0.273 ± 0.153	1.78
Fruit of standard size	Open branches	−0.612 ± 0.289	−2.12*
	Seeds	0.385 ± 0.060	6.41***
Fruit of standard shape	Seeds	0.291 ± 0.040	7.37***

Notes: Fixed effects included, as appropriate: branch treatment, pollination system, pollination service × branch treatment combination, number of flowers (flowers), and number of seeds (seeds). In all models, farm was included as the random variable (groups = 12). *denotes $p < 0.05$; ** denotes $p < 0.01$, and *** denotes $p < 0.001$.

experiments to hectare-scale yield estimates introduces uncertainty, these results remain informative for illustrating the influence of pollination source on apple production profitability.

The average 2024 price for fresh apples (local and export) was USD 748 per tonne, while the price for processed apples was USD 131 per tonne (Table 3).

At an aggregate scale, extrapolated values indicated that excluding insect pollination resulted in an average of nine apples per tree, compared with 181 when insect pollination was available (Table 3). Insects are therefore an essential production factor for apples.

In terms of quality, managed pollinators yielded the highest fresh-to-processed apple ratio of 1.9:1 (i.e., almost two apples for the fresh market for every apple destined for processing).

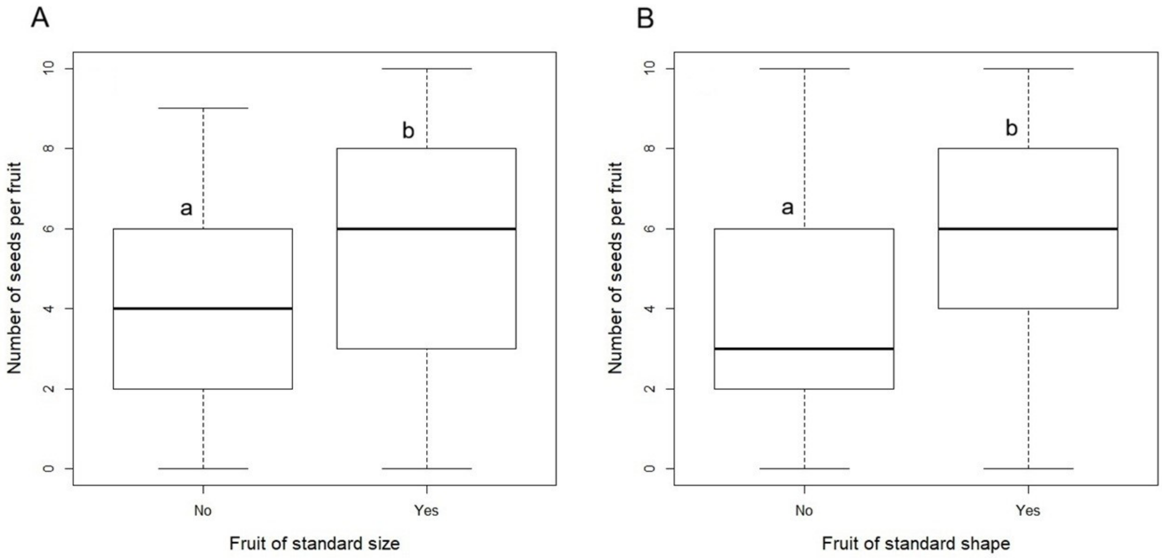

Figure 2. Relationship between fruit quality and explanatory variables as indicated by: (A) fruit of standard size (industry specification of passing through a 60 mm hoop), and (B) fruit of standard shape (symmetrical and not lopsided). Both are expressed as binary responses with "No" and "Yes" indicating not meeting and meeting the industry standard, respectively. Different letters (a and b) indicate significant differences between responses at $p < 0.001$.

Table 3. The financial value of insect pollination for farmers using one of three different pollination source options available to growers

Variable	Managed pollination source only		Both pollination sources		Wild pollination source only		Insect pollination excluded	
Trees (ha^{-1})	1,248		1,291		1,302		1,280	
Flowers (tree^{-1})	2,020		2,558		1,760		2,113	
Mean fruit set	8		8.75		9		0.42	
Fruit grade	Fresh	Processed	Fresh	Processed	Fresh	Processed	Fresh	Processed
% grade	65.6	34.5	47.1	52.9	48.2	51.8	34.0	66.0
Mean fruit number (tree^{-1})	106	56	105	118	76	82	3	6
Mean fruit weight, g	127.1	88.2	129.8	102.4	139.3	117.1	126.0	103.7
Yield (ha^{-1}), t	16.80	6.13	17.67	15.65	13.85	12.51	0.48	0.77
Market price (t^{-1})	USD 747.7	USD 131.2	USD 747.7	USD 131.2	USD 747.7	USD 131.2	USD 747.7	USD 131.2
Income per produce grade	USD 12,560.7	USD 804.2	USD 13,211.2	USD 2,053.2	USD 10,355.1	USD 1,641.3	USD 358.9	USD 101.0
Total income (USD ha^{-1})	USD 13,365.0		USD 15,264.4		USD 11,996.4		USD 459.9	
Value as % of max income	87		100		78		3	

Notes: As a reference, orchard yield in the absence of pollination was also calculated and scaled up from pollinator exclusion experiments. Both quantity (yield) and quality (marketable versus processed fruit) were considered in the valuation.

Scenario 2 (employing both managed and wild pollinators) had the highest yield (33 tonnes per hectare) and the highest income (USD15,264 per hectare). Although scenario 1 (managed pollinators only) had the lowest yield among the three scenarios (23 tonnes per hectare), it achieved the second-highest income per hectare (USD 13,365). Scenario 3 (wild pollination only) ranked second in yield (26 tonnes) but third in income (USD 11,996 per hectare) (Table 3). These differences clearly illustrate both the price-effect (the price differential between fresh and processed apples) and the yield effect (the ratio of fresh to processed apples). Although, in theory, lower yields of high-quality fruit can outperform higher yields of lower-quality fruit in terms of total income per hectare, it was not the case here.

In terms of cost–benefit, the cost of renting a managed pollination service at two hives per hectare (stocking density) was only USD 118 per hectare. Consequently, income from orchards using hived honey bees (USD 13,247 and 15,146 per hectare) exceeded income from orchards not renting hives (USD 11,996 per hectare).

4. Discussion

We found that apple orchards with deployed hives had greater honey bee visitation, resulting in superior fruit quality (fresh-to-processed ratio). Furthermore, proximity to wild pollinator habitat had little effect on pollination levels, despite the orchards being located in a biodiversity hotspot with many potential wild pollinator species. In sum, we show that the managed pollination service using hived endemic honey bees is at least as efficient as the ecosystem service provided by wild pollinators and that the insurance factor from hived bees is a major factor in the commercial production of high-quality (i.e., financially favorable) apples.

These results therefore rejected our hypothesis that managed and wild pollination regimes are comparable in terms of the efficiency and quality of pollination services. The deployment of hived bees was by far the best approach, even though a few wild individuals might also have been present, unlike in typical pollination studies.[6,7] We also did not find any synergistic interaction between having both hived bees and wild pollinator habitat around the orchards. This suggests that in our study, there is a negligible additional contribution to pollination from both wild honey bee colonies, which likely occur at lower densities than the hive stocking density, and other wild pollinators, due to their low observed abundance on apple flowers in the orchards.

4.1. Quality comparison of wild and managed pollination services

Our results confirmed the overall importance of effective insect pollination for apples. However, contrary to other studies, reliance on managed pollination (notably an endemic bee) rather than wild pollination resulted in both superior pollination and fruit quality. At the other end of the spectrum, and consistent with Mallinger and Gratton,[17] we found that exclusion of insect pollinators resulted in a marked reduction in pollination success, affecting both initial and final fruit set, as well as the number of seeds per apple. This is consistent with the finding that most apple cultivars require insect-pollination.[43]

Flowers with access to insect pollinators, regardless of pollination source, resulted in successful initial and final fruit set, and these did not differ significantly among the three pollination treatments used in orchards. In turn, the number of seeds per apple affected the minimum size requirements and fruit shape. Shape depends largely on the number of seeds set during the pollination process, with a low number of seeds per fruit leading to abnormal apple growth and lower-quality fruit,[43-45] with seed set being considered a more direct measure of pollination efficiency than fruit weight.[46] Thus, overall, despite similar fruit-set, apples were of marginally better quality when managed honey bees were used compared to reliance solely on wild pollinators (wild honey bees and other pollinators).

4.2. Flower visitation patterns

Presence of other bees or flower-visiting insects during our sampling window was negligible (only 1.2%). The large difference in visits between honey bees and all other wild pollinators is extreme but is in line with an unpublished apple dataset (study number 84) used in Kleijn *et al.*'s[47] meta-analysis, which is from the same production area. Surveying 800 minutes in 10 Royal Gala orchards (five close and five distant [≤1 km and ≥2 km, respectively] from natural vegetation) in October 2011, a total of 2,132 honey bees but only 34 non-honey bee flower visitors were observed on apple blossoms (respectively an average of 2.67 and 0.04 visits min^{-1}), with one individual of *Xylocopa* sp. being the only other bee species recorded. In Kleijn *et al.*'s[47] apple dataset, honey bees accounted for 99.1 % of all flower visitations, which compares favorably with the 98.8% found in our study. Admittedly, the observation time could have been increased to five minutes in our study. However, the relative abundance of honey bees would remain unchanged. As we did not set out to document pollinator biodiversity, any species that were missed would have a lower abundance and a small effect on the ecosystem service of pollination. It has been shown by Kleijn *et al.*[47] that many pollinator species (even bees) do not contribute significantly to pollination ecosystem services, with only a few species providing most of the pollination service.

Comparing our and previous results, Isaacs and Kirk[48] found that for highbush blueberries, wild bees were the dominant pollinators in small fields, comprising 58% of flower-visiting bees, whereas 97% of bees in large fields were honey bees. Therefore, our figure of 99% honey bee visitors is in keeping with these findings. Also on blueberries, Blaauw and Isaacs[49] adjusted their pollinator efficiency estimate for wild bees to provide 82% of the pollination in small fields, but only 12% of the total pollination services across their whole blueberry system. They found that providing forage habitat for bees adjacent to pollinator-dependent crops can conserve wild pollinators in otherwise resource-poor agricultural landscapes when about half of the surrounding landscape is natural. In comparison, Blitzer *et al.*[10] documented a 50:50 ratio of honey bees to wild bees in apple orchards in the United States of America (USA), with all orchards close to natural areas. In turn, Klein *et al.*[4] showed that honey bees account for 70% of all flower visitors sampled in intensive Californian almond orchards bordering, or far from, natural areas, with flower strips next to orchards having little ameliorating effect on wild pollinators when there is little semi-natural habitat in the surrounding vicinity.

We did not find greater honey bee visitation or seed set in orchards with access to both pollination services than in those relying solely on managed honey bee pollination. That the same number of hives is introduced in these two types of orchard pollination systems suggests only a small number of honey bees are entering from natural vegetation surrounding the orchard, especially as very few honey bees were recorded in orchards when no hives were introduced. Potentially, there could be resident honey bee hives in the non-natural areas interspersed between orchards or immediately bordering them. However, one would then expect the outcome to be universal across all our apple orchards. As orchards that received no hived bees had such low honey bee visitation, this strongly suggests that this potential additional source of wild honey bees is negligible.

4.3. Implications for apple growers in the study area

The observed difference between the pollination services provided by wild versus hived honey bees is likely due to wild colonies still building up to full strength following winter (in addition to having to fly farther to the orchard from natural areas), and assumes no adverse weather or competition from wild flowers. Deciduous crops such as apples, pears, and plums all require cold for synchronized flowering and optimal fruit production management.[43,50] It is also worth noting that, unlike the native vegetation surrounding apple orchards in the USA,[10] CFR vegetation lacks a significant proportion of native Rosaceae species, whereas in the former, apple orchards are surrounded by native Rosaceae trees. One would thus expect a better match between wild pollinators serving native plants and those serving crop species. Consequently, in our study, the demand for pollination is not necessarily synchronized with the peak of local pollinator supply (wild honey bees and other pollinators). In contrast, hived bees can be moved onto alternative forage sources to build up hive strength, thereby being independent of on-farm conditions.[51] The timing of this is likely to vary slightly from year to year according to spring temperatures. However, even if in some years there are sufficient wild pollinators (wild honey bees and other pollinators) to provide a satisfactory pollination service, growers cannot rely on such an unpredictable service. Given the insignificance of the costs of managed pollination relative to overall apple production costs (about 1%),[22] the risks are simply too great to leave pollination to chance, and consequently, hived honey bees are now routinely employed.[23,52,53]

Today, there are almost no apple orchards in the CFR that do not use hived honey bees for pollination, despite many orchards directly bordering substantial patches of natural vegetation. This is emphasized by the fact that in the production year following our study, three of the four orchards relying solely on wild pollination changed their pollination service use by importing hived honey bees, and have continued to use this service ever since. This suggests that growers do not consider bordering natural habitat reliable enough to safeguard yield and therefore rent managed honey bees. If farmers can outsource the pollination service required per hectare to a beekeeper, at about 1% of their production cost, why would they take on this responsibility themselves?

Our recommendation is that, instead of growers relying on wild pollination services from adjacent natural areas (e.g., Klein *et al.*[4]), they should invest in ensuring a sustainable supply of hived honey bee colonies for their industry.[38,53] This is essential because reliance on a single pollinator species carries risks due to disease susceptibility and the availability of the service market.[8,54] However, we are not suggesting that enhancing pollination by planting indigenous flower strips in CFR apple orchards should not be considered, as such a management option can also enhance pollination and fruit production,[55] making the two approaches complementary.

4.4. Comparing our case study to more typical pollination ecosystem service studies

Most pollination ecosystem service studies investigate the effects of wild pollinators, and often honey bees, on fruit set. They typically do not select study areas where isolation from natural habitat, or a low percentage of natural habitat surrounding the crop, would result in almost no wild pollinators,[6,7,56] nor do they assess whether there might be risk factors associated with wild pollinators. However, farmers growing insect–pollinator-dependent crops under such conditions must introduce managed pollinators; otherwise, yields would be zero.[12,14] This creates a bias when comparing hived honey bees and wild pollinators in crop systems where a substantial proportion of wild pollinator habitat is present. Here, we take a different perspective and view the pollination service provided by hived indigenous honey bees for safe fruit production as a service chosen by the grower, with all commercial apple growers in the study area now adopting this option.

Blitzer *et al.*[10] raise similar questions regarding apple pollination, and Mallinger and Gratton[17] compare orchards that use or do not use managed honey bees. However, all their orchards had access to large numbers of wild bees, and introducing managed honey bees into these "full" orchards is unlikely to significantly increase pollination.[17] Here, we focused on the converse: what is the pollination success under conditions of negligible numbers of wild pollinators but with the introduction of managed honey bees under our "pollinator-poor" conditions? Predictably, as shown by Blitzer *et al.*[10] and Mallinger and Gratton[17] found, wild bees in northern USA are important for apple pollination. However, the situation in CFR is different: hived endemic honey bees make an economically viable contribution while ensuring growers that crop failure will not occur. Nonetheless, there remains potential value in applying complementary practices (e.g., flower strips, semi-natural habitat buffers) that may enhance wild pollinator abundance without replacing the managed service currently used.[55]

Our case study highlights two points that are often not acknowledged in typical pollination ecosystem service studies, while supporting some highlighted by Isaacs *et al.*[19] First, as illustrated here, many hectares of pollinator-dependent crops are cultivated in intensive agricultural areas that lack significant sources of wild pollinators and therefore depend solely on managed pollination for commercial production.[4,14,19] Some crops have pollination requirements and/or are grown under agri-environmental conditions that necessitate the use of managed pollinators. This means that, despite some wild pollinators being more effective per visit in fruit set than honey bees in many parts of the world,[6] when managed honey bees are the dominant (> 90%) flower visitors, they are likely to cumulatively contribute more to crop pollination than the more efficient wild pollinators.[18,57] Second, even when crops are located close to wild pollinator habitat, this does not guarantee a viable pollination ecosystem service. For example, adverse weather conditions may reduce wild pollinator abundance levels insufficient for a financially viable pollination ecosystem service.[58,59] De Palma *et al.*[60] show that although pollination ecosystem services can be influenced by several bee assemblage diversity traits, the relative importance of each facet is largely determined by the study system. Broad generalizations can therefore give a biased view of wild insects' ability to provide insurance when managed pollination becomes unavailable.[6,8] Our study may represent a special case in which a native-managed pollinator provides the bulk of a crop pollination service. Therefore, the sustainable management of natural resources for agricultural production requires careful study and explicit acknowledgment of the local context.

5. Conclusion

This study presents a finding contrary to much of the pollination services literature regarding the simultaneous use of managed and wild pollination services—namely, the assumption that wild pollinators can replace the service provided by managed honey bees. In this case, the presence of natural habitat near the crop did not ensure sufficient pollination by wild pollinators. The use of hived native honey bees in the CFR should therefore be considered an essential input for high-quality apple production. Furthermore, growers are advised to use managed honey bees as a pollination service insurance policy to guarantee fruit production, regardless of the orchard's proximity to natural areas. Importantly, the managed pollinator in our study was the Cape honey bee, which is endemic to the region, with beekeepers typically trapping wild swarms to replenish lost colonies. Our study emphasizes why locally collected data should take precedence over broad international policy recommendations and demonstrates why context matters in the optimal use of pollination services.

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Conflict of interest

The authors declare that they have no competing interests.

Author contributions

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Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data

The dataset is available from the corresponding author upon reasonable request.

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Appendix

Table A1. Mixed model selection for explaining honey bee flower visitation, pollination success, and fruit quality dependent variables for 12 apple orchards

Dependent Variable					
Model	**AIC**	**ΔAIC**	**SD$**	**Dev/df**	**Fixed effects**
Number of honey bee foragers					
Model 1	1,014	-[a]	0.731	3.1	Pollination service + wind
Model 2	1,016	2[b]	0.753	3.1	Pollination service
Initial fruit set					
Model 1	2,498	1[a]	0.464	4.4	Pollination service branch treatment
Model 2	2,497	-[a]	0.460	4.4	Pollination service branch treatment + flowers
Model 3	2,509	12[b]	0.467	4.4	Branch treatment
Final fruit set					
Model 1	1,934	-[a]	0.393	3.6	Pollination service branch treatment + flowers
Model 2	1,938	4[b]	0.389	3.6	Branch treatment + flowers
Model 3	1,942	8[b]	0.386	3.6	Pollination service + branch treatment + flowers
Number of fully formed seeds					
Model 1	2,438	-[a]	0.184	4.4	Pollination service branch treatment
Model 2	2,464	26[b]	0.179	4.5	Pollination service + branch treatment
Model 3	2,470	32[c]	0.276	4.5	Branch treatment
Normal fruit size					
Model 1	521	-[a]	1.393	0.94	Seeds + branch treatment
Model 2	523	2[b]	1.275	0.94	Seeds
Model 3	524	3[b]	1.080	0.94	Seeds + pollination service
Normal fruit shape					
Model 1	663	-[a]	0.475	1.2	Seeds
Model 2	663	-[a]	0.482	1.2	Seeds + branch treatment
Model 3	665	3[b]	0.432	1.2	Seeds + pollination service

Notes: Models for each variable were ranked according to the lowest Akaike information criterion (AIC) or the lowest number of variables in the model (if ΔAIC < 1). The farm was included as a random effect in all cases (12 groups). Dev/df indicates the ratio of residual deviance to residual degrees of freedom. Branch treatment: closed versus open; pollination system: managed versus managed + wild versus wild; pollination service × branch treatment combination: managed closed and open, managed + wild closed and open, wild closed and open. $ denotes the standard deviation of the random factor. Different letters (a, b, and c) indicate significant differences between models at $p < 0.05$.

Table A2. Summary statistics of apples collected from marked branches in three types of apple pollination systems

Type of pollination	Number of apples harvested from marked branches		Average fruit weight		Average number of seeds per fruit	
	Fresh	Processed	Fresh	Processed	Fresh	Processed
Managed only	79	41	127.1	88.2	7.7	5.7
Both types	57	64	129.8	102.4	6.4	5.2
Wild only	82	87	139.3	117.1	5.6	4.4
Pollinators excluded*	69	134	126.0	104.5	4.6	3.0

Notes: *Important to note that the number of fruits indicated for insect-excluded apples is not indicative of the reduction in apple production. Rather, the data represent the quality of fruit that was actually harvested and not the quantity. All netted branches were also summed and averaged to indicate the importance of insect pollination for fruit quality.

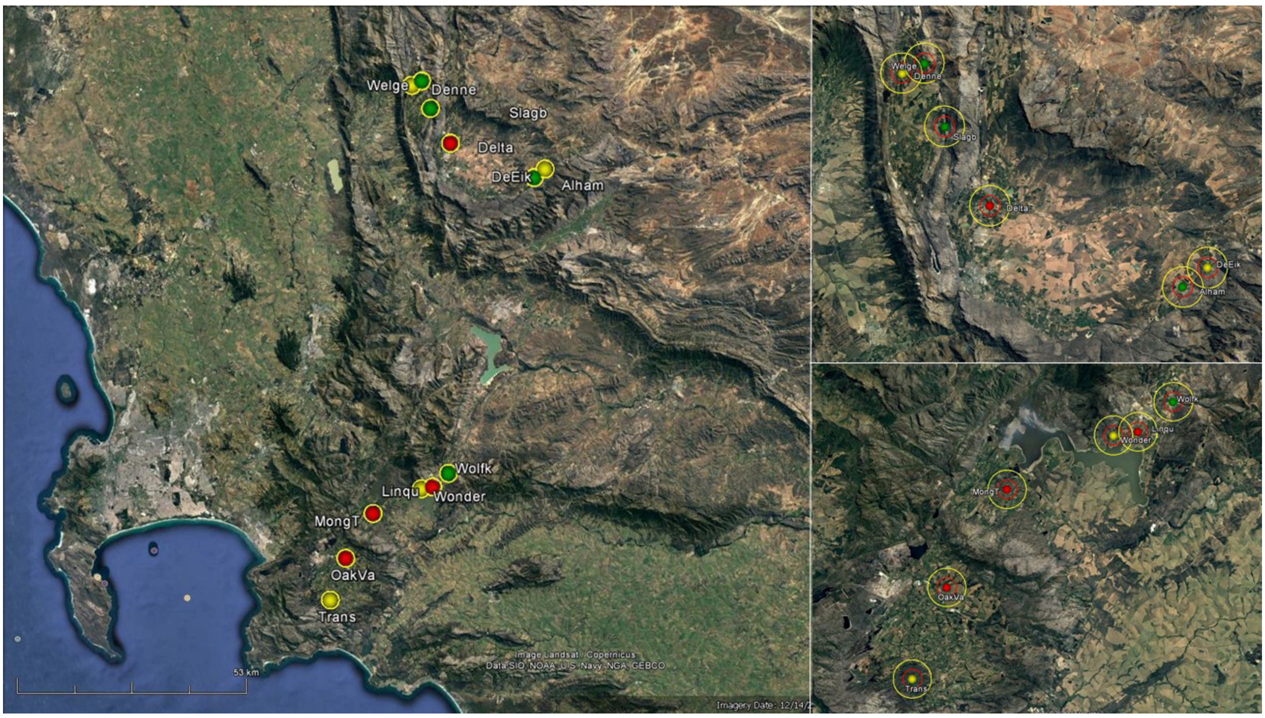

Figure A1. Geographical map showing location of our study orchards, with zoomed-in inserts of the six northern and six southern study sites/areas (orchards), respectively. Red, yellow, and green dots indicate orchards using managed, wild and managed, and wild pollination services, respectively. Red and yellow circles indicate buffer areas of 1 km and 2 km radius around each sampled orchard, respectively. Images show landscapes viewed from Google Earth © 2017 Google.