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Proximity to natural habitat and flower plantings increases insect populations and pollination services in South African apple orchards

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Abstract

1. Introducing areas of wildflower vegetation within crop fields has been shown to enhance pollinator activity and pollination services to crops, and findings in Europe showed an interaction effect between floral treatments and landscape context. Natural fynbos patches in the South African Cape Floristic Region (CFR) are potential reservoirs for beneficial insects that could enhance pollinator populations and crop pollination in commercial apple orchards. However, the effect of proximity to natural habitat and floral enhancement treatments on crop pollinators and yield are yet to be fully tested in southern temperate regions.
2. To elucidate the impact of enhanced floral resources to apple flower visitors and crop yield, we established small experimental patches of flowers in non-productive areas of commercial apple *Malus domestica* orchards in the CFR. Experimental orchards were embedded in landscapes with varying proportions of natural habitat within 1 km. We used pollinator exclusion experiments to determine the benefits of insect pollination on apple yield, quality and economic value.
3. We found that the primary pollinator of apple flowers in the region is the endemic Cape honey bee, *Apis mellifera capensis*. Floral plantings enhanced overall pollinator abundance and honey bee flower visitation within the orchards, and positively affected apple size and economic value. Increased landscape complexity had a significantly positive effect on wild bees but not on honey bees.
4. *Synthesis and applications*. We demonstrate that presence of floral plantings within orchards enhances pollinator activity within apple orchards and apple quality. This sustainable management practice may represent a profitable choice for growers, which could increase pollination services while reducing reliance on renting hives. These practices can indirectly contribute to increased landscape-scale resilience and connectivity while also benefiting pollinators within the remaining natural habitat.

KEYWORDS
apple quality, bees, crop yield, ecosystem services, natural habitat, pollination, South Africa, wildflowers

1 | INTRODUCTION

Animal pollination is required for most of the world's flowering plants (Ollerton et al., 2011) and plays a key role in agroecosystems worldwide, where it enhances yield of many crops (Klein et al., 2007). Wild insects are highly efficient pollinators of several crops (Rader et al., 2016) and provide pollination insurance in the face of *Apis mellifera* (hereafter 'honey bee') losses (Potts et al., 2010). However, wild insect populations are undergoing a severe global decline in both wild and agricultural landscapes (Potts et al., 2016; Seibold et al., 2019), where habitat loss, fragmentation and agricultural intensification are significant drivers of pollinator decline (Sánchez-Bayo & Wyckhuys, 2019). Many farmers worldwide respond to pollinator scarcity by renting beehives (Aizen & Harder, 2009), particularly honey bees. However, reliance on a single species is inherently risky, given challenges facing honey bees (Breeze et al., 2014; Pirk et al., 2014).

Growing evidence suggests that integrating floral resources into farms increases both abundance of wild insects and the services they provide (Blaauw & Isaacs, 2014; Tscharntke et al., 2012). This is usually achieved by sowing mixes of native grassland flower species on arable land (Carvell et al., 2004), and, in Europe, it forms part of Agri-Environment Schemes (Pywell et al., 2006). Furthermore, the effects of floral enhancement areas are moderated by landscape structure (Tscharntke et al., 2012), where the effectiveness of local management on insect abundance and species richness is higher in structurally 'simple' landscapes (ones with fairly low proportions of semi-natural habitats) than in complex or extremely simplified landscapes (Scheper et al., 2013).

While ecosystem services and their management are increasingly well understood in north temperate agroecosystems, they are only partially investigated in the global south (Steward et al., 2014). Some pollination management studies have been conducted in South America and East Asia and Pacific (e.g. Arthur et al., 2010; Pérez-Méndez et al., 2020) and previous studies have explored the effect of wildflower planting on mango and sunflower in parts of South Africa (Carvalheiro et al., ,2011, 2012). Furthermore, the beneficial impact of non-crop floral resources on beneficial arthropods communities in apple orchards has been studied in Europe (Campbell et al., 2017; Fitzgerald & Solomon, 2004; García & Miñarro, 2014), yet similar research from sub-Saharan Africa on apple and other crop types is sparse, despite it being an important reservoir of global biodiversity and the demanding human food requirements (Steward et al., 2014).

Wild pollinators in natural settings have been widely investigated in the insect-rich Cape Floristic Region (CFR) in South Africa (e.g. Adedoja et al., 2018; Kehinde & Samways, 2012; Vrdoljak & Samways, 2014). However, to our knowledge, the effect of habitat enhancement on pollinators in South African apple orchards remains untested. Here we determined what impacts floral planting and landscape complexity have on the insect pollinators in South African orchards, and whether they are comparable to those in north temperate agricultural landscapes. We hypothesise that flower visitor abundance, fruit yield and quality measures, and economic value would increase in apple trees adjacent to floral plantings, and that these benefits would be greater in orchards surrounded by simple landscapes.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted in apple orchards in the Elgin, Grabouw, Vyeboom and Villiersdorp (EGVV) pome fruit (apple and pear) growing region of the Western Cape Province, South Africa, in 2018 (Figure 1). This region is within the CFR biodiversity hotspot, a global centre of terrestrial biodiversity (Goldblatt & Manning, 2000). Natural fynbos is a local sclerophyllous vegetation, dominated by Proteaceae, Ericaceae and Restionaceae, and especially rich in local endemic plant and insect species. The study area contains large areas of high conservation value within protected areas such as the Kogelberg Biosphere Reserve, as well as in privately owned areas (Grant & Samways, 2011; van Schalkwyk et al., 2019). The Western Cape region is also a prime zone for agriculture, comprising 93% of the total national pome fruit production area.

The study was carried out in 36 commercial apple orchards growing the Golden Delicious cultivar. This cultivar makes up 23% (5,522 ha) of the total apple planted in South Africa, and is the most exported cultivar (Hortgro, 2018). We identified orchards embedded in a gradient of natural habitats (NH) within a 1 km radius around each experimental orchard (i.e. a 1 km buffer), which ranges between 8% and 77% of area cover (Figure 1). NH were described using the DEA National Landcover 2015 dataset (DEA, 2016) while the buffer around the orchards was delineated in the Cape Farm Mapper (WCDA, 2017). Percentage NH was calculated as the sum of non-agricultural woody, wetland or natural/semi-natural terrestrial land-use classes (3, 4, 5, 6, 8 and 9).

To test the benefits of floral planting, we established three 40-m long transects in each orchard, perpendicular to the field edge and spaced >25 m apart. Along each transect, we created three, evenly spaced (14 m apart), 2 m × 1 m floral plots placed in the middle of the work row between tractor tyre paths (Figure 1). Floral treatments consisted of (a) a 'simple' transect planted with plots of Sweet Alyssum *Lobularia maritima*; (b) a 'diverse' transect with plots planted with a mixture of 11 different flower species (Table S1); and (c) a

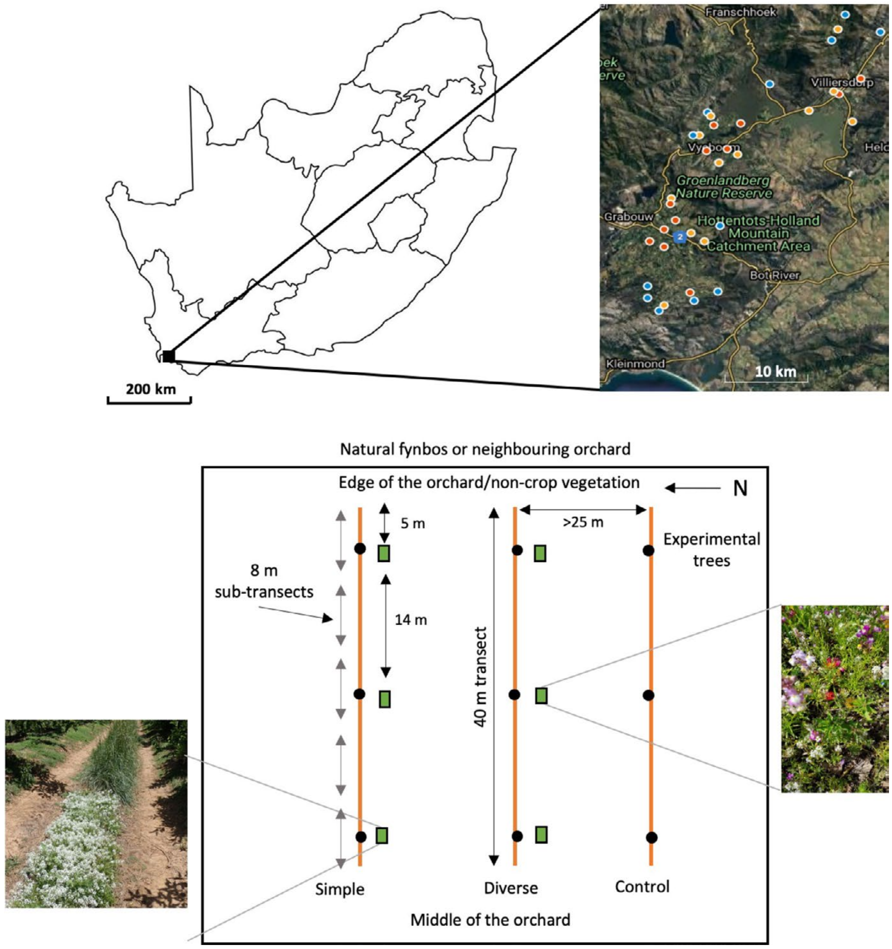

FIGURE 1 Top: the study area located in the Western Cape Province of South Africa, located about 70 km north-west of Cape Town. Locations of the 36 experimental orchards are categorised by the proportion of natural habitat in the 1 km radius: Low (red), Medium (yellow) and High (blue). Bottom: orchard experimental layout (bottom image) with position of floral planting and experimental trees

control consisting of un-manipulated plots typical orchard management (i.e. grass). *Lobularia maritima* was selected for its relatively long flowering period and attractiveness for a broad spectrum of pollinators (Gómez, 2000).

2.2 | Flower visitor observations

Visitation surveys on apple blossoms were conducted on two separate days during peak flowering time to determine the effect of floral planting and landscape complexity on apple pollinators. Observations were carried out between 10:00 and 16:00 hr along each transect in dry weather with temperatures 13℃ or more and wind speed less than Beaufort scale 5 (<29 km/hr). Transects were further divided in five by 8-m long sub-transects, which were recorded as independent samples to test if floral visitation decreased towards the centre of the field as seen on other crops (Woodcock et al., 2016). Each flower visitor was recorded to broad taxonomic groups (e.g. honey bee, other wild bee, hoverfly, other fly, beetle, ant, Lepidoptera) and noted only if each individual made contact with the flower's reproductive parts (hereafter 'pollinator'). To establish the total floral area of each planted plot, we recorded the number of open flowers in the floral plots twice over the flowering period. The total floral area per plot was calculated by multiplying the average area of the flower head of each species by the number of flowers of that species that were open at the time of recording. The endemic honey bee *Apis mellifera capensis* occurs in the region both in wild and managed population, as bee hives are heavily supplied to orchards during the flowering season. To account for the influx of supplied honey bees, the number of beehives within a 1 km radius from the edge of the orchards was recorded during field surveys and their distance to the experimental transects measured from satellite imagery.

2.3 | Insect assemblage sampling

To assess differences in beneficial insects between orchards and non-crop areas, and test for any interaction between floral treatments and landscape composition, we conducted two rounds of pan-trapping between November 2018 and January 2019. Triplicate pan traps consisted of 85 mm wide coloured bowls (neon blue, neon yellow and bright white) each with a glossy glaze coat acrylic sealer to enhance durability and marked with three centrally intersecting 10 mm wide black guide lines (Wilson et al., 2016). Traps were placed in the middle of each floral plot, as well as 5 m into the non-crop vegetation opposite to the end of the transect.

2.4 | Apple fruit yield and quality

Following Garratt, Breeze, et al., (2014), we carried out pollinator exclusion experiments to determine dependence of apple production on insect pollination. From the closest tree to the centre of each flowering plot (*c*. 2 m), three accessible branch ends were randomly selected, and then randomly assigned to one of three treatments: (a) un-manipulated, flowers accessible to wind, insect and self-pollination (control treatment); (b) enclosed in a 45 cm × 30 cm mesh bag (1 mm) to prevent insect pollinators accessing flowers (bagged treatment); and (c) flowers hand-pollinated using pollen collected from the orchard's polliniser variety. Prior to manipulation, we recorded number of flowers on each branch. Bags were placed before flowers opened and removed at the end of the flowering period to minimise microclimatic and pest exclusion effects. Overall, 972 branches from 324 trees were assessed.

Apples were collected immediately prior to harvest and cold stored. To assess fruit set, yield and quality, the following variables were measured within 2 weeks of storage: maximum width, firmness, fresh weight, number of seeds, number of locules, starch and sugar content.

2.5 | Economic valuation

We calculated the market value of pollination based on the estimated crop yield and quality of each pollination treatment, and in the presence or absence of floral plantings, using an average of market prices for export and local market (Hortgro, 2018). See Table S2 for calculation details and apple grading criteria.

2.6 | Statistical analyses

Poisson generalised linear mixed-effects models (GLMM) were used to investigate the effect of landscape context and floral planting on abundance of apple flower visitors. We categorised flower visitors into two groups: honey bees only, and other visitors (non-honey bees), which were treated as two distinct response variables. Landscape context (% NH cover in 1 km buffer), floral planting type (simple, diverse and control), floral area, distance from orchard's edge and hives index (see below) were fixed effects (Table 1). Recorder, orchard identities and date were included as random effects in the model, the latter to account for repeated observations. Models were specified using all possible combinations of all the explanatory variables and one interaction between landscape and floral area.

We selected the best models as those with the lowest values of Akaike's information criterion (AIC, Burnham & Anderson, 2002). For all top performing models (ΔAIC < 2), we calculated model averaged estimates and unconditional 95% confidence intervals (CI) with multimodel inference (Burnham & Anderson, 2002). We standardised all the continuous variables and tested for multicollinearity (VIF < 2; Graham, 2003). Effects were considered significant when the 95% CI for parameter estimates did not overlap zero.

To account for excess zeros in non-honey bee visitors, we fitted GLMMs, zero-inflated GLMMs, and hurdle models with Poisson and negative binomial distributions on the conditional models (Brooks et al., 2017). The full zero-inflated GLMMs allows both the conditional and zero-inflation models to differ between fixed factors included in each model (Brooks et al., 2017).

The same models were fitted to pan trap data, which also had an excess of zeros. We performed two separate analyses on pan trap catch data: (a) we used the entire dataset to test differences in all insect abundance between orchards and non-crop areas and (b) we analysed pan trap catches in the orchards alone to elucidate the effect of landscape context and floral planting on insect abundance. The best models were selected as those with the lowest values of AIC (Burnham & Anderson, 2002).

To account for the density of managed beehives (*A. mellifera capensis*) that are placed around orchards during flowering time, we used number of hives and their distance from the experimental transects to calculate a 'hives index', using the formula:

$$Dj = \frac{N_j}{\text{meandistance}^2},$$

where Dj is the hives index, N_j is the number of hives in 1 km radius and meandistance^2 is the mean distance of the hive to the middle experimental transect. The hives index was used as a random effect in analyses.

We evaluated differences between apple yield (fruit set and fruit number) among pollination treatments using binomial and Poisson GLMMs, respectively. In all models, the manipulated tree identity nested within floral transect nested within orchard, and recorder were random effects and pollination treatments were fixed effects. Using the same model structure, we also tested the effect of landscape context, floral planting, their interaction, and distance from orchard's edge on fruit set and fruit number of open pollinated branches.

Effect of pollination treatments on apple quality firmness, mass, width, starch content (square root transformed) and sugar content (square root transformed) was evaluated using linear mixed-effect models (LMMs). Pollination manipulation unit (branch end) nested within tree nested within orchard were random factors and pollination treatment was the fixed factor (Table 1). Effect of landscape context, floral planting, their interaction and distance from orchard's edge on fruit quality was tested on apples exposed to normal insect activity (open pollination), using LMMs. Post-hoc Tukey tests were used to assess differences in yield and quality measures between pollination treatments.

Model assumptions were verified by plotting residuals against fitted values and for each covariate in the model. Statistical analyses were conducted in R version 3.1.2. (R Core Team, 2019) with the packages LME4, MUMIN and GLMMTMB (Barton, 2011; Bates et al., 2015; Brooks et al., 2017).

TABLE 1 Explanatory variables included in the mixed-effects models with subcategories, which were used as sublevels in the analysis

Explanatory variables	Subcategories	Details	Question addressed
Fixed factors			
1. Landscape context		Proportion (%) of natural habitat occurring within a 1 km radius from the orchard	Effect of natural habitat in the surrounding landscape on flower visitor abundance and consequent fruit yield and quality
2. Floral planting type		3 by 40 m long transects per orchard, each sown with three 2m×1m sown plots placed in the middle of the orchard's workrow: Simple = transect with plots sown with Sweet Alyssum *Lobularia maritima* Diverse = transect with plots sown with a mixture of 11 different flower species (Table S1). Control = unmanipulated control transect with plots of grass or typical orchard management	Effect of the type of floral resources within orchards on flower visitor abundance and consequent fruit yield and quality
3. Floral area		Floral cover area in each planted plot, measured in m^2	Effect of enhanced floral resources within orchards on flower visitor abundance and consequent fruit yield and quality
4. Distance from orchard's edge	Sub-transectA Sub-transectB Sub-transectC Sub-transectD Sub-transectE	The three experimental transects (2. floral planting type) were divided in 8 m long sub-transects where A is by the field edge (5 m) and E is in the middle of the orchard (40 m) Flower visitor abundance was collected independently in each transect	Edge effect on floral visitation
5. Pollination treatment	Bagged Open Hand	Open Control = unmanipulated control flower buds Bagged = flower buds covered in 1 mm mesh bags Hand Pollination = flower buds were hand pollinated with pollen collected from the orchard's pollinisers	Effect of pollinators on fruit yield and quality
6. Position of experimental tree	Edge Middle End	Location of the experimental trees along each transect Edge = by the edge of the field Middle = in the middle of the transect End = far end of the transect, towards the middle of the field The location of the experimental trees corresponded to the position of the three floral plots	Effect of distance from orchard's edge on fruit set and fruit number of open pollinated branches
Random factors			
1. Hives index		Number of hives/square mean distance from experimental transect	
2. Date		Dates in which data were collected	
3. Recorder		Recorder's name	
5. Tree identity		ID number of trees with manipulated branches	
6. Orchard identity		Name of experimental orchards	

3 | RESULTS

3.1 | Flower visitor observations

Overall, we observed 6,039 insect individuals on *M. domestica* in the 36 apple orchards for a total of 72 hr. Bees were the most abundant visitors: 89% of total visitors were wild/managed honey bees, 1% were other bees, 4% were hoverflies, 1% were beetles and 4% lepidopterans. Beehive density was consistent across the experimental orchards (0.0011 *SE* ±0.0002).

Honey bee abundance was positively affected by increasing distance from the edge of the field, and with increasing floral area between orchards rows (Figure 2A; Table 2). Models showed a 15% increase in honey bee abundance for every 1 m^2 of floral cover. Proportion of natural habitat within a 1 km radius did not have a significant effect on honey bee abundance (Table 2; Table S3). Non-honey bee abundance, however, responded positively to landscape complexity, increasing sharply by 35% with a 10% increase in natural habitat within a 1 km radius (Figure 2B; Table 3; Table S4).

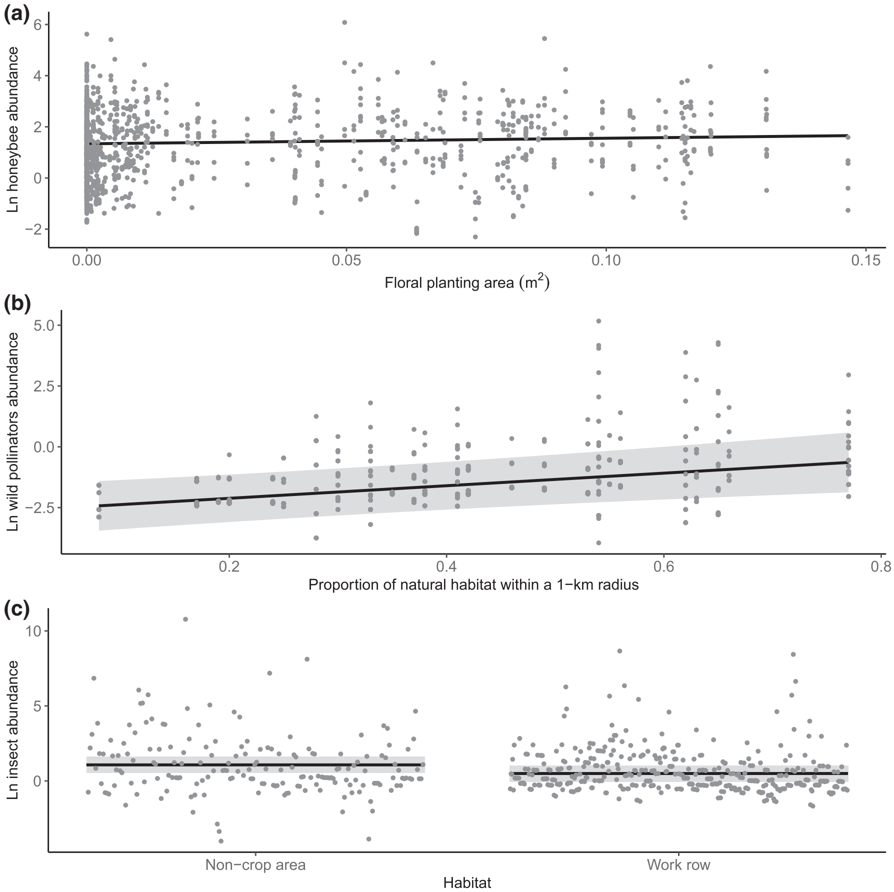

FIGURE 2 Relationship between (A) honey bee abundance per transect and floral area, (B) non-honey bee abundance per transect and landscape context and (C) all insect abundance per catch and the habitat in which pan traps were placed (Work row = inside the orchards, Non-crop area = non cultivated area just outside the orchard edge). Confidence intervals are indicated by the shaded areas

TABLE 2 Logged model-averaged estimates (β) of explanatory variables with unconditional ±*SE* and 95% unconditional confidence intervals for Poisson GLMM models explaining the abundance of honey bees flower visitors per transect in the apple orchards of the CFR, South Africa (see Table S3 for all candidate models)

			95% confidence interval	
Variable	**ß**	***SE***	**Lower limit**	**Upper limit**
Intercept	**1.401**	**0.227**	**0.955**	**1.848**
Distance edge	**0.067**	**0.028**	**0.011**	**0.124**
Floral area	**0.143**	**0.070**	**0.004**	**0.282**
Flower simple	**−0.089**	**0.037**	**−0.163**	**−0.016**
Flower diverse	−0.056	0.097	−0.248	0.135
Landscape	0.213	0.178	−0.136	0.564

Note: Estimates whose unconditional 95% confidence intervals do not overall zero are shown in bold.

3.2 | Insect assemblage sampling

Pan trap catches comprised Halictidae, Megachilidae and Colletidae species belonging to Apidae (*A. mellifera capensis* 11.7% of total catch) and Syrphidae. The model with a significant effect of floral area and landscape context best explained the variation of insect abundance inside the orchards (Table 4a; Table S5a). Furthermore, pan traps inside the orchards had about 43% less insects than those in the non-crop area (Table 4b; Figure 2C; Table S5b).

3.3 | Apple fruit yield and quality

A total of 1,680 fruits were collected from the exclusion experiments out of a total of 972 manipulated branches. Fruit set depended on pollination treatment (χ^2 = 151.49, p < 0.001), and the post-hoc Tukey test revealed a significant difference between all pollination treatments (Figure 3A).

Open pollination conditions resulted in a fruit set of 44% while excluded flowers and hand pollinated flowers resulted in a 20%

TABLE 3 Logged estimates (β), *SE* and 95% confidence intervals of the fixed effects included in the best model (zero-inflated Poisson model) explaining the abundance of non-honey bee flower visitors per transect in the apple orchards of the CFR, SA (see Table S5 for all candidate models)

Variable	ß	*SE*	95% confidence interval: Lower limit	95% confidence interval: Upper limit
Intercept	**−1.929**	**0.418**	**−2.749**	**−1.109**
Landscape	**3.000**	**0.820**	**1.392**	**4.607**
Distance edge	—	—	—	—
Floral area	—	—	—	—

Note: Estimates whose unconditional 95% confidence intervals do not overall zero are shown in bold.

TABLE 4 Logged estimates (β), *SE* and 95% confidence intervals of the fixed effects included in the best model (Negative binomial, ΔAIC < 2), explaining the abundance of beneficial insects in pan trap catches across (a) apple orchards and surrounding non-crop; and (b) pan trap catches within the orchards in the Cape Floristic Region, South Africa (see Table S5 for all candidate models.)

Fixed effect	ß	*SE*	95% confidence interval: Lower limit	95% confidence interval: Upper limit
(a)				
Intercept	−0.066	0.266	−0.588	0.454
Habitat—orchard	**−0.575**	**0.104**	**−0.780**	**−0.370**
Landscape	**1.389**	**0.569**	**0.273**	**2.504**
(b)				
Intercept	**−1.12**	**3.13**	**−1.74**	**−0.50**
Floral area	**4.26**	**1.64**	**1.03**	**7.5**
Landscape	**2.02**	**6.89**	**0.81**	**3.3**

Bold values indicate statistical significance ($p < 0.001$).

and 49% fruit set, respectively (Figure 3A). Fruit number was significantly greater following hand pollination and open pollination compared to pollinator exclusion ($\chi^2 = 559.72$, $p < 0.0001$), which yielded on average less than one fruit per branch end (0.5 *SE* ±0.06; Figure 3B). Landscape complexity, floral planting and distance from orchard edge did not affect the fruit set and fruit number of naturally pollinated branches.

Exclusion experiments showed that pollination treatment had a significant effect on all quality measures (Table 4). Open pollinated apples were on average 8.6% heavier and 4.7% bigger than apples from pollinator excluded branches (Figure 3C,D; Table 5). Hand pollinated apples had a significantly greater number of seeds than open and excluded apples (Figure 3E; Table 5). Sugar content of fruits that had been isolated from flower visitors was significantly lower than in those under open pollination (Figure 3F) and was below the 11.7% threshold for Class 1/2 apples. Finally, open pollinated apples adjacent to greater floral area cover were significantly bigger ($\chi^2 = 5.44$, $p = 0.019$). We found that apples on trees adjacent to floral plantings were on average 1 mm larger than those with no floral plantings nearby, yielding about 10% more Class 1 size apples (≥60 mm).

3.4 | Economic value of pollination services

Fruit number, weight and proportion of Class 1 Golden delicious apples were substantially higher in the open treatment compared to the closed treatment. Gross return of the open treatments increased by R170 328 per ha (*c*. $9,000). This translates into a total added gross return across South Africa of R 941 m (*c*. $50 m). Hand pollination yielded a potential increase in gross return of approximately R52 000 (*c*. $2,800) per ha, suggesting a potential pollination deficit of R287 m ($15,200) on a national scale. The increased potential gross economic value attributable to floral plantings was calculated to be about R4 160 per ha (*c*. $220).

4 | DISCUSSION

This is the first study to quantify the impact of floral enhancement on apple orchard insects and on both yield and quality of this economically important crop in South Africa. Our results suggest that creating small floral patches in non-productive areas of apple orchards can support wild and managed pollinators and increase crop quality of adjacent apple flowers. Region-specific studies are vital to inform conservation and management strategies, as even the same crops may respond differently to farm management in different agro-ecological contexts (Kehinde et al., 2018).

Consistent with previous research (Carvalheiro et al., 2012; Kennedy et al., 2013), beneficial insects responded positively to addition of floral resources inside the orchards. This is likely due to the additional foraging resources supporting pollinator persistence (Roulston & Goodell, 2011). However, in contrast with observations in other temperate regions (e.g. Garratt, Breeze, et al., 2014; Garratt, Truslove, et al., 2014), most visits to apple flowers were carried out by the endemic honey bee *A. mellifera capensis*. This is surprising given the great diversity of bee species inhabiting the CFR (Kuhlmann, 2005) and that apple flowers in more biodiversity poor regions are visited by a wider variety of species (Blitzer et al., 2016; Martins et al., 2015). Given that honey bee visits accounted for 89% of the total visits, wild bees may be affected in their foraging behaviour and by the competition with high densities of managed honey bees (Mallinger et al., 2017), and be outcompeted on apple flowers.

Honey bee abundance was not influenced by the isolation from natural habitat in the surrounding landscape. Conceivably, they are less dependent on floral and nesting resources in the immediate surroundings due to hive supplementation, their relative resilience to agricultural intensification and ability to move greater distances

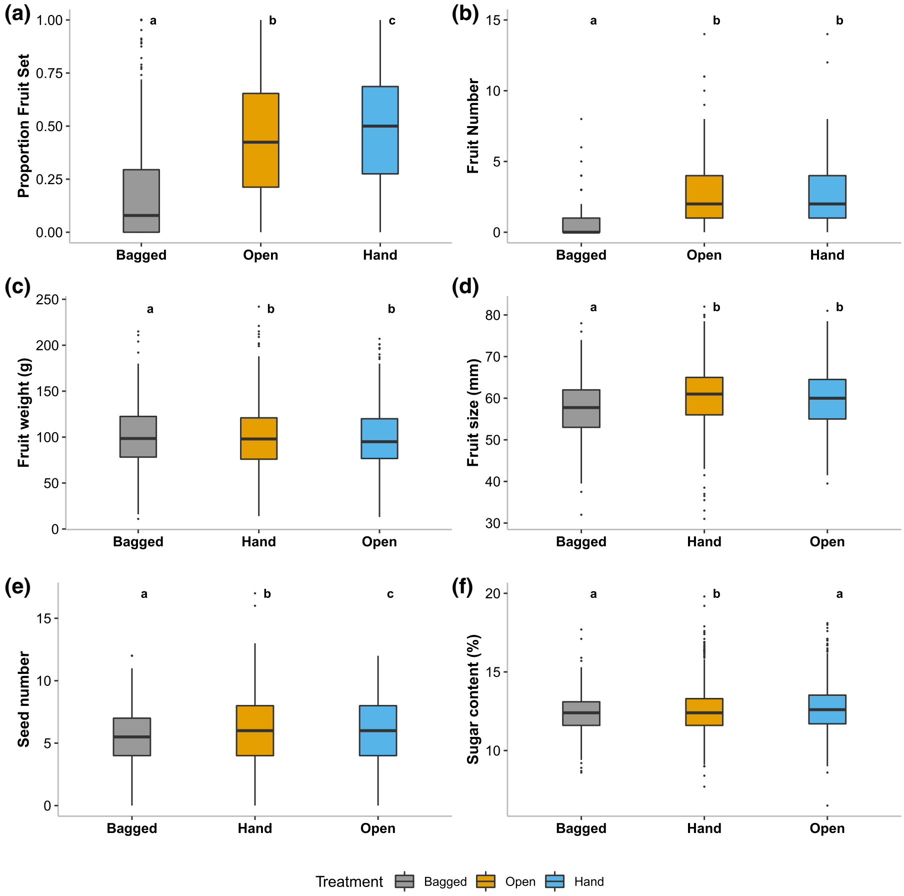

FIGURE 3 Effect of pollination treatment on: (A) apple fruit set per branch; (B) fruit number per branch; (C) fruit weight measured in grams; (D) fruit size measured as the maximum length (mm), (E) seed number and (F) percentage of sugar content. The medians, 1st and 3rd quartiles for the three treatments are shown. Error bars represent upper and lower quartiles. Mixed-effect models show that pollination treatment had a significant effect on all quality measures, different letters above bars represent significant differences

compared to smaller bees (Kleijn et al., 2015). Conversely, landscape complexity was a strong predictor of non-honey bee pollinator abundance on apple flowers, with greater activity in orchards surrounded by higher proportions of natural habitat. This is supported by a large body of research showing the negative effect of isolation from natural habitat on wild pollinators (Garibaldi et al., 2011; Kennedy et al., 2013). The steep effect of natural habitat on non-honey bee species within the orchards can be explained by their reduced ability to disperse due to their smaller body size compared to honey bees (Greenleaf et al., 2007). Contrary to the findings of Scheper et al. (2013), we found no significant interaction effect between landscape complexity and floral enhancement practices. This may be due to a lack of strong contrast between our landscape categories with simple and complex landscapes following a continuum rather that a defined contrast.

Wild bees in pan traps were positively affected by floral planting within orchards. This is consistent with existing evidence that the effectiveness of practices such as floral enhancement is more strongly related to local ecological contrast than landscape context (Marja et al., 2019). These enhanced habitats may play a key role as forage and refuge resources and support the long-term persistence of beneficial insects and the ecosystem services they provide to crops.

Exclusion of flower visitors to apple greatly reduced fruit set and number, confirming the high dependence of apple on animal-mediated pollination (Garratt, Breeze, et al., 2014; Garratt, Truslove, et al., 2014) and providing evidence of the crucial importance of insect pollination for apple production in South Africa. When comparing open and pollen supplementation treatments, we found a potential pollination deficit in seed number, which is positively related to other quality measures such as size and shape (Buccheri & Vaio, 2005).

We found that insect abundance, but not yield measures, was enhanced by floral planting in orchard systems as suggested elsewhere (Campbell et al., 2017). This may be because, following floral enhancement practices, a time lag of two or more years is often needed to allow populations of service-providing insects to build up before any effect on yield can be detected (Kleijn et al., 2019). Despite this, we found that added floral resources within the orchards increased apple size even with relatively small-scale floral treatments, which has significant consequences for orchard management. While fruit number and size deficits can be partly managed by adjusting the thinning regime, the potential increase in apple size may result in a substantial economic return for a relatively low cost.

TABLE 5 Effect of pollination treatment on apple quality measures. Means ± *SE*, Chi-square and *p* value were extracted from the linear mixed-effects models

Quality measure	Pollinator exclusion	Open pollination	Hand pollination	*df*	χ^2	*p* value	Significant difference
Width (m)	57.41 ± 0.9	60.10 ± 0.59	60.43 ± 0.58	1672	32.78	<0.0001	Hand > Bagged Open > Bagged
Mass (g)	92.28 ± 4.1	100.25 ± 2.5	102.6 ± 2.5	1672	16.79	<0.0001	Hand > Bagged Open > Bagged
Sugar (%)	11.62 ± 0.01	13.69 ± 0.02	11.61 ± 0.02	1672	1,035.2	<0.0001	Hand > Open Open > Bagged
Starch (%)	24.60 ± 0.22	29.26 ± 0.18	31.47 ± 0.17	1672	14.45	<0.0001	Hand > Bagged Open > Bagged
Firmness	8.7 ± 0.1	8.38 ± 0.1	8.28 ± 0.1	1672	30.35	<0.0001	Bagged > Hand Bagged > Open
Seed number	2.17 ± 0.26	3.26 ± 0.24	4.41 ± 0.24	1672	302.82	<0.0001	Hand > Bagged Open > Bagged Hand > Open
Number of Locules	5.30 ± 0.07	5.38 ± 0.09	5.28 ± 0.18	1672	6.49	=0.03	Open > Hand

Multi-year, full orchard-scale experiments are required to assess the optimal amount of floral resources needed at orchard level and to elucidate the full benefits of enhanced floral resources on measurable yield and quality effects.

The lack of landscape effect on the measured production variables is in keeping with the meta-analysis of Herbertsson et al. (unpublished/under review), who found no clear link between plant reproductive success and landscape simplification at a global scale. Presumably, a modest effect of landscape complexity on floral visitation is further diluted by a modest level of pollination deficit, producing an effect of landscape simplification on reproductive success that is too small to be detected.

4.1 | Conservation and management implications

We demonstrate here the ability of added floral resources to enhance pollinator activity within apple orchards and increase apple size. Yet in-field management practices, including floral enhancement, are often the least preferred by farmers (Kleijn et al., 2019). Growers may be reluctant to add floral resources to the orchards due to the costs involved and the belief that the coexistence of crop and non-crop flowers would lead to competition and reduce the efficiency of their pollination investment (M. Addison, pers. comm.). This could pose a potential barrier in adopting these sustainable practices, which have been demonstrated to be effective elsewhere in the world for the enhancement of regulating ecosystem services (Winfree et al., 2007). Here, we found no evidence of competition, and the plantings facilitated pollination by increasing abundance of beneficial insects inside the orchards. Our study provides context-specific evidence against this belief, and by disseminating the results to the farming community, it may contribute to changing the growers' attitude to these management practices.

Furthermore, our results confirmed the high economic value of insect pollination in apple production, as seen in previous studies (Garratt, Breeze, et al., 2014; Garratt, Truslove, et al., 2014; Geslin et al., 2017) and show a potential gross return attached to floral planting of about R4 160 per ha (*c.* $220). Our estimates are not to be taken as a full cost–benefit analysis as they do not take into account direct costs such as the cost of establishment and maintenance of floral plantings. However, providing estimates of the potential economic returns of habitat enhancement practices and the absence of risk to production may raise interest among growers and increase the adoption of these practices.

Currently, apple production in South Africa is highly dependent on managed endemic honey bees, where virtually all orchards are supplemented at a density of *c.* 2 hives per ha (Allsopp et al., 2008). This exposes the industry to a substantial risk in a system where the bee keeping is already under stress (Pirk et al., 2014). Habitat loss caused by climate change, the increasing frequency of fires and eucalyptus removal reduces important foraging resources for wild and managed bees throughout the year (Adedoja et al., 2019; De Lange et al., 2013), and pathogens and diseases are known stressors for bee keepers (Allsopp, 2004). Increasing managed pollinator efficiency through the augmentation of in-farm floral resources could reduce the number of hives required per unit area of orchard. Thus, reducing unsustainable demands on the bee-keeping industry, reducing hive hiring costs and, most importantly, making pollinations services more resilient to variable climatic regimes by reducing system exposure to future stresses and shocks. Greater insect diversity may intensify behavioural interactions between wild and managed bees and increase pollination efficiency as in other crop systems (Greenleaf & Kremen, 2006). Furthermore, the endemic *A. mellifera capensis* favours many of the local fynbos flowers over apple flowers as pollen and nectar sources (Addi et al., 2006), hence enhancing orchard floral resources might encourage managed bees to forage in orchards for longer instead of moving into the fynbos.

Ultimately, adopting biodiversity-friendly practices in orchards at a landscape level can have the double benefit of contributing to increased landscape-scale resilience and connectivity for pollinators within the remaining natural habitat (Driscoll et al., 2013) and enhancing crop productivity and profitability.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

W.K., M.J.S., R.G., J.S.P., S.M.S. and P.S. conceived the research, P.S. oversaw the data collection, F.R. analysed the data with input from P.S., W.K. and S.M.S.; All authors contributed to ideas and interpretation of results; F.R. led the writing of the manuscript with input from all authors. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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