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Floral resource strips enhance parasitoid abundance and diversity in apple orchards and promote agroecological advances in a South African biosphere reserve

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Abstract

1. Agricultural intensification drives insect declines, including that of parasitoids, through landscape simplification and extensive use of synthetic pesticides. Spatially heterogeneous agricultural landscapes are potentially important biodiversity reservoirs where non-crop habitats may support populations providing ecosystem services to farming. However, there is a need to find methods to support this transition to more sustainable farming and support the progressive concept of biosphere reserves.
2. We focus here on the relationship between apple orchards and sclerophyllous natural fynbos vegetation in the megadiverse Kogelberg Biosphere Reserve, Cape Floristic Region, South Africa. We established patches of floral resources within apple orchards, which are embedded in landscapes, equivalent to the transition zone of the Kogelberg Biosphere Reserve (KBR), with varying proportions of natural habitat in a 500-m radius around orchards. We assessed the role of these enhanced floral resources for supporting parasitoid abundance, species richness and diversity inside orchards and compare these metrics to those in ruderal vegetation around orchards and in nearby natural vegetation. Further, we assessed the effect of semi-natural vegetation in the surrounding landscape mosaic on parasitoids in orchards.
3. Floral enhancement improved parasitoid abundance and influenced assemblage composition within apple orchards. However, non-crop ruderal habitat immediately adjacent to orchards supported greater abundance and richness of parasitoid species, while natural fynbos supported even richer parasitoid assemblages. Vegetation within orchards and landscape complexity enhanced parasitoid assemblages inside and surrounding the orchards.
4. Our study shows that increasing floral resources within orchards improves local diversity of parasitoids within agroecosystems in the Biosphere Reserve. In doing so, this improves levels of biodiversity and increases parasitoid richness within the biosphere transition zone, supporting a shift from conventional production to a more biodiversity-friendly agroecological approach.

KEYWORDS
biosphere reserve, ecosystem services, floral patches, metabarcoding, natural enemies, planted flowers

INTRODUCTION

Agricultural intensification involves conversion of natural and semi-natural habitat for agricultural use, reduction of crop diversity and simplification of agricultural landscapes and is one of the major threats to arthropod biodiversity worldwide (Batáry et al., 2020; Foley et al., 2011; Habel et al., 2019).

From a biodiversity conservation perspective, this is concerning. In response, there has been a shift away from conventional agriculture towards promoting agroecological initiatives which support biodiversity conservation, including that of insects (Gaigher, Pryke, et al., 2024; Gaigher, van den Berg, et al., 2024). One way to do this is to instigate set-asides of suitable vegetation between the rows of woody crops (Winter et al., 2018). While there has been a focus on beneficial parasitoids for pest control (Lérault et al., 2022), there is a dearth of information on overall parasitoid diversity in set-asides, our focus here.

Evidence from various regions also suggests that improved landscape structure of crop areas (in terms of increased plant heterogeneity and potential resources) has a positive influence on farmland biodiversity, sometimes reaching levels that are comparable to those of nearby natural/semi-natural vegetation (Aguilera et al., 2020; Alignier et al., 2020; Sirami et al., 2019). For example, floral resources within farms may increase the prevalence of natural enemies, such as parasitoids and hoverflies, consequently enhancing pest control (Albrecht et al., 2020; Blaauw & Isaacs, 2012). Furthermore, landscape structure can moderate the effect of floral plantings on insect abundance and species richness (Tscharntke et al., 2012). Proportionately greater effects are seen in structurally 'simple' landscapes (with a low percentage of semi-natural habitats) compared to either complex (with higher proportions of such habitats) or extremely simplified landscapes (with none) (Scheper et al., 2013). Furthermore, enhanced, non-crop floral resources benefit the pollinator guild in apple orchards in Europe (Campbell et al., 2017; Fitzgerald & Solomon, 2004; García & Miñarro, 2014).

The studies above come from the global north, with similar patterns also emerging in the global south. In South Africa, for instance, improvements in the landscape structure of semi-natural vegetation and within vineyards can improve arthropod diversity (Gaigher, Pryke, et al., 2024; Gaigher, van den Berg, et al., 2024), while semi-natural field margins can support high predator diversity in maize agroecosystems (Botha et al., 2015, 2018). Furthermore, the close proximity of natural vegetation to South African mango and oranges promotes natural enemy diversity, benefiting pest control in the crop (Galloway et al., 2021; Henri et al., 2015).

An innovation to support more biodiversity-friendly farming has been undertaken by the United Nations Educational, Scientific and Cultural Organisation's *Man and the Biosphere Programme* (https://www.unesco.org/en/mab). This is an international initiative that promotes the establishment of biosphere reserves globally. Biosphere reserves provide logistical support for the conservation of the natural functions of biodiversity, while also supporting sustainable development (Pool-Stanvliet et al., 2018), including that of food production, the focus here. Globally, there are currently 759 BRs in 136 countries, with 10 in South Africa and four within the biodiversity-rich Cape Floristic Region (CFR) at the southwestern tip of South Africa: Cape Winelands Biospehere Reserve (BR), Kogelberg BR, Cape West Coast BR and Garden Route BR (Samways et al., 2024a).

Each biosphere reserve consists of three zones. There is a central core zone that embraces full biodiversity conservation, principally through designation of a formally protected area. Surrounding the core is a buffer zone, intended to protect the core zone, and where only low-impact land use is permitted, such as agroecological farming, sustainable harvesting of natural resources and tourism, as well as natural areas. The outermost zone is the transition zone (investigated here) which supports more extensive human activities, although agroecological farming and sustainable practices are encouraged. The CFR's biosphere reserves zones aim to integrate and harmonise agricultural production while conserving the exceptionally rich biodiversity heritage. However, as the zones in practice have indistinct edges and are largely delineated according to existing human activities and conservation initiatives, there is room for improvement through identification of further practices that make agriculture more biodiversity friendly, our aim here. In the CFR, various approaches have been investigated to promote arthropod diversity including the setting aside of land such as abandoned agricultural patches, mostly vineyards, to benefit parasitoids (Gaigher et al., 2016) and spiders (Theron et al., 2020a), by increasing cover crop to promote overall arthropod (Gaigher, Pryke, et al., 2024; Gaigher & Samways, 2010; Gaigher, van den Berg, et al., 2024) and improving cover crop and management to enhance arthropod diversity (Geldenhuys et al., 2021, 2022a, 2022b, 2022c) and to enhance insect-flower interaction networks (Kehinde & Samways, 2014; summarised in Samways et al., 2024a).

The CFR biodiversity hotspot supports very high levels of both endemic plant species (Goldblatt & Manning, 2000) and arthropod species (Janion-Scheepers et al., 2020; Kemp & Ellis, 2017; Procheş & Cowling, 2006; Samways et al., 2024b). The natural 'fynbos' vegetation is sclerophyllous, dominated by Proteaceae, Ericaceae and Restionaceae. However, over 30% of the CFR land surface has been converted to agriculture and urbanisation, reducing the primary natural vegetation to 17% (Cowling et al., 2003; Rouget et al., 2003). The dominant agriculture is deciduous fruit production and vineyards (Greeff & Kotze, 2007), many of which are intensively managed, putting great pressure on local biodiversity (Esler et al., 2014).

Our focus here is on the transition zone of the Kogelberg Biosphere Reserve, where apples are the dominant fruit, and so we investigate one approach to integrate apple production and biodiversity conservation in this reserve. We do this because the CFR is an important reservoir of global biodiversity while also a centre for fruit production. To date, few studies have examined agroecological innovations that support both biodiversity and food production (Steward et al., 2014). In the case of pollinators, Ratto et al. (2021) showed that floral plantings enhance overall pollinator abundance and activity within orchards, leading to improved fruit quality. However, the potential impact of agroecological enhancements on beneficial natural enemies, and potential pest control ecosystem services, has not been explored in food production systems embedded within biodiversity hotspots. Here, we assess the impact of floral plantings, especially their floral area and habitat type on parasitoid assemblages both within the orchards and in the surrounding habitat. We hypothesise that parasitoid abundance, species richness and diversity within apple orchards would increase with increasing floral availability and that increasing the area of semi-natural habitat at the landscape scale would have a positive effect on parasitoid assemblages in the farms.

METHODS

Study area, sites and experimental design

Our study took place in 2018 in the Kogelberg Biosphere Reserve in the heart of the CFR and was South Africa's first biosphere reserve, designated in 1998. This biosphere reserve has core terrestrial areas in the formally protected Kogelberg and Groenlandberg Nature Reserves, mostly in the mountainous areas. The core zone has extremely high levels of biodiversity and endemism (Johns & Johns, 2001) and is bordered by a buffer zone of mostly natural and near-natural vegetation. In turn, the transition zone consists mostly of conventional deciduous fruit production.

We selected 36 commercial apple orchards with the Golden Delicious cultivar (Figure 1) in the transition zone of the Kogelberg Biosphere Reserve, where the overall aim was to move away from conventional production and embrace agroecological approaches. The study orchards were interspersed with large areas of high conservation value within privately owned areas (Grant & Samways, 2011; van Schalkwyk et al., 2019).

We identified orchards embedded in a gradient of natural habitats within a 500-m radius (i.e., a 500 m buffer), which represents the average flight distance for small hymenopterans in agricultural landscapes (Evans, 2018). We selected 12 orchards in each of these landscape classes: (1) High in natural habitat (>50%), (2) Medium in natural habitat (between 30 and 40%) and (3) Low in natural habitat (<20%). Overall, the percentage of natural vegetation area for all sampled orchards in the 500 m orchard buffer ranged between 8% and 77% (Figure 1). Natural habitat cover was determined using the Department of Environmental Affairs National Landcover 2015 dataset (DEA, 2016), while the buffer around the orchards was delineated in the Cape Farm Mapper (WCDA, 2017). Percentage natural habitat 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) (Table S1).

The floral plantings

Three 40-m-long transects were established in each orchard to assess the relationship between floral plantings and the diversity and abundance of natural enemies (parasitic Hymenoptera) that are floral visitors. Transects were placed in the inter-rows between the planted rows of apple trees, perpendicular to the field edge and spaced >25 m apart.

Following Ratto et al. (2021), we created three, evenly spaced (14 m apart), 2 m × 1 m floral plots placed along each transect in February 2018 (Figure 1). Floral treatments consisted of (1) a 'simple' transect planted with plots of Sweet Alyssum (*Lobularia maritima*), which was selected due to its relatively long flowering period and attractiveness to a broad spectrum of beneficial insects (Gomez, 2000; Urbaneja-Bernat et al., 2024); (2) a 'diverse' transect with plots planted with a mixture of 11 different flower species (Table S2) and (3) a 'control' consisting of unmanipulated plots of typical orchard management (i.e., mostly various grasses and some weeds). We also established single sampling sites at the end of each transect, 5 m into the adjacent semi-natural vegetation. These sites were not florally enhanced; they were intensely managed and regularly trimmed. They consisted of ruderal vegetation, mostly grass and little to no floral resources. The fynbos is a shrubland with exceptional levels of plant endemism and forms part of the CFR. Flowering occurs in spring (September to November), with a variety of flower forms present. We use the term 'non-crop habitat' for these sites. Additionally, we included single sampling sites in remnant, natural fynbos vegetation in the broader landscape.

The number of open flowers in the floral plots was recorded twice over the flowering period to determine the total floral area of each planted plot. We calculated the total floral area per plot 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 sampling (Ratto et al., 2021).

Parasitoid sampling

We carried out two rounds of pan-trapping for parasitoids between November 2018 and January 2019 to test the effect of floral treatments and habitat type on comparative parasitoid abundance, species richness and diversity (Shweta & Rajmohana, 2018). Pan trap catches were also used to evaluate differences in parasitoid assemblages between orchards, non-crop areas and fynbos in the surrounding transition zone landscape.

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 guidelines (Wilson et al., 2016). Traps were placed in the middle of each floral plot, as well as 5 m into the non-crop vegetation at the end of the transect and within patches of natural fynbos in the wider landscape. This design resulted in 324 pan trap arrays in orchards (36 orchards × 3 transects × 3 treatments), 108 pan trap arrays in non-crop vegetation (36 orchards × 3 transects × 1 plot) and 18 pan trap

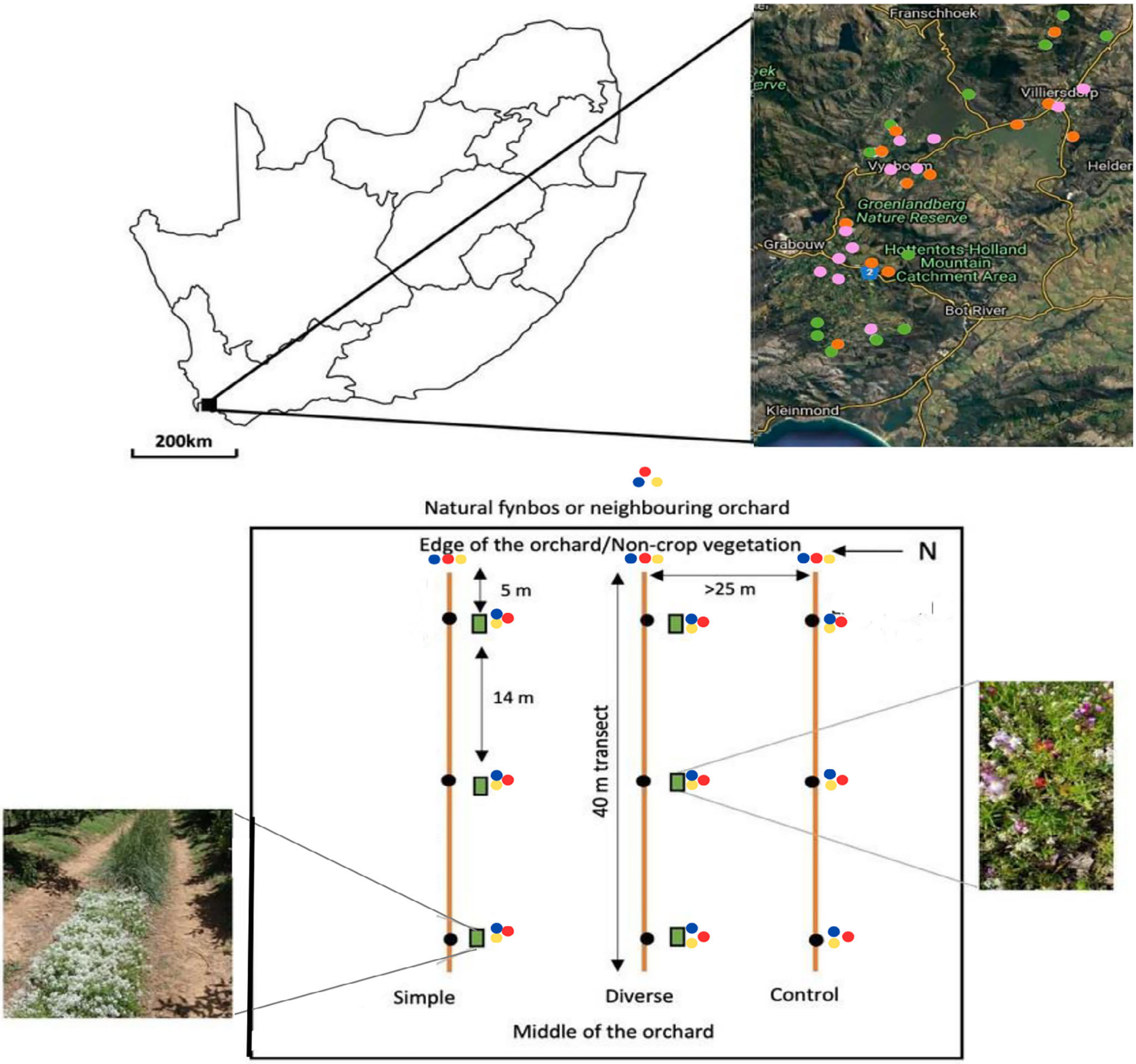

FIGURE 1 Top left: map showing the study location in the Western Cape Province of South Africa. Top right: 36 experimental orchards colour-coded based on the proportion of natural habitat within a 500 m buffer of each orchard: low (pink), Medium (orange), High (green). Bottom: experimental layout of orchards with position of transects, floral planting (green rectangles) and pan traps (blue, red and yellow dots). Traps were placed adjacent to the floral planting, at the end of each transect, 5 m into the adjacent natural area, and within patches of natural fynbos in the wider landscape (modified from Ratto et al., 2021).

arrays in fynbos (placed ad hoc, depending on accessibility). The contents of the pan traps were then individually filtered with sterile filter paper to isolate the specimens from the liquid. Filter papers with specimens were then stored in 96% ethanol at 4°C. All hymenopteran parasitoids were extracted for further analysis.

Molecular and parataxonomic identifications

Composition of parasitoid assemblages was identified using the HAMI (Human Assisted Molecular Identification) framework described in Penel et al. (2025). This approach takes advantage of COI metabarcoding for the identification of complex insect assemblages in combination with a parataxonomic validation of the outputs. This is appropriate for the rich and poorly known CFR fauna of hymenopteran parasitoids, as it enables the rapid recognition of relevant morphospecies into mOTUs (molecular operational taxonomic units) reflecting the species composition of a given sample. It also gives precise abundance data for each species, which is not possible in standard metabarcoding approaches. Following this protocol, each sample was first sorted into RTUs (recognisable taxonomic units) traditionally identified morphospecies, imaged and then set in a 96-well plate for molecular identification. The metabarcoding protocol followed the two-step PCR strategy detailed in Galan et al. (2018) and was complemented by the dual-index paired-end sequencing methodology outlined in Kozich et al. (2013). The DNA of each bulk sample was extracted non-destructively using a 96-Well Plate Animal Genomic DNA Miniprep Kit (Biobasic) following the manufacturer's instructions, except for the initial lysis step conducted overnight to ensure the extraction of DNA from hard-bodied groups of Hymenoptera (i.e., Chalcididae). Also, one extraction blank (NCE) was consistently incorporated. The first PCR (PCR1) was then conducted in an 11-μL reaction volume, using 5 μL of 2× Qiagen Multiplex Kit Master Mix (Qiagen), 0.5 μM of each forward and reverse primer and 2 μL of DNA extract. This PCR amplified a 133 bp fragment of the mitochondrial COI gene (primer pair: MG-L CO1490 5′-ATTCHACDAAYCAYAARGAYATYGG-3′ and MG-R 5′-ACTATAAAARAAAYTATDAYAAADG CRTG-3′) suitable for species discrimination in parasitic Hymenoptera (Sow et al., 2018). The second PCR (PCR2) used PCR1 products and added to the amplicons multiplexing indices and Illumina sequencing adapters. In each microplate, one PCR blank (NCPCR) was consistently incorporated. The PCR2 products (3 μL) were checked through electrophoresis on a 1.5% agarose gel and then pooled. The resulting libraries were then paired-end sequenced (two runs) on Illumina MiSeq flowcells using MiSeq Reagent Kit v2 (500 cycles), with a sequencing length of 300 bp which implies partial overlap of paired-end reads. Details regarding PCR steps, annealing temperatures and post-sequencing bioinformatic processing are in Penel et al. (2025). MOTUs were identified to family level using the Genbank (https://www.ncbi.nlm.nih.gov/genbank/).

Finally, the imaged RTUs were confronted with MOTUs (morphological operational taxonomic units) by a parataxonomist (JH) in a reconciliation step for the removal of false and true positives (molecular amplification bias or contamination) and a record of abundance.

Statistical analyses

To test the effect of floral plantings and habitat type on parasitoid abundance and species richness, we fitted Poisson generalised linear mixed-effect models (GLMMs) on the pan trap catches within the orchards. The full model contained floral area, habitat type (% natural habitat area cover in 500-m buffer as a continuous variable) and floral planting type (control, simple, diverse) as fixed factors.

Sampling period and floral planting type nested in orchard identities were included as random effects (Table 1). The model with the lowest values of Akaike's information criterion was chosen as the best model (AIC, Burnham & Anderson, 2002). Model average estimates and unconditional 95% confidence intervals (CIs) with multi-model inference for all top performing models were calculated (ΔAIC < 2, Burnham & Anderson, 2002). Effects were considered significant when the 95% CI for parameter estimates did not overlap zero.

TABLE 1 Explanatory variables included in the generalised and linear mixed-effects models.

Explanatory variables	Details	Question addressed
Fixed factors		
1. Landscape complexity (continuous)	Proportion (%) of natural habitat occurring within a 500-m radius from the orchard.	Effect of natural habitat in the surrounding landscape on parasitoids abundance, species richness, diversity and species composition
2. Landscape complexity (categorical)	Proportion (%) of natural habitat occurring within a 500 m radius from the orchard divided into three categories: (1) High natural habitat (>50%) (2) Medium natural habitat (between 30% and 40%) (3) Low natural habitat (<20%)	
2. Floral planting type	3 by 40 m long transects per orchard, each sown with three 2 m × 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 parasitoids abundance, species richness, diversity
3. Floral planting area	Floral cover area in each planted plot, measured in m^2	Effect of enhanced floral resources within orchards on parasitoids abundance, species richness, diversity and species composition
Random factors		
4. Orchard identity	Name of experimental orchards	
5. Sampling round	(1) in November 2018; (2) in January 2019	

A linear mixed-effects model (LMM) was fitted to evaluate the effect of the selected environmental variables on the Shannon and Simpson diversity index within the orchard. The Shannon diversity index was used to account for species richness and rare species and the Simpson's diversity index to account for evenness and dominance (Shannon, 1948; Simpson, 1949).

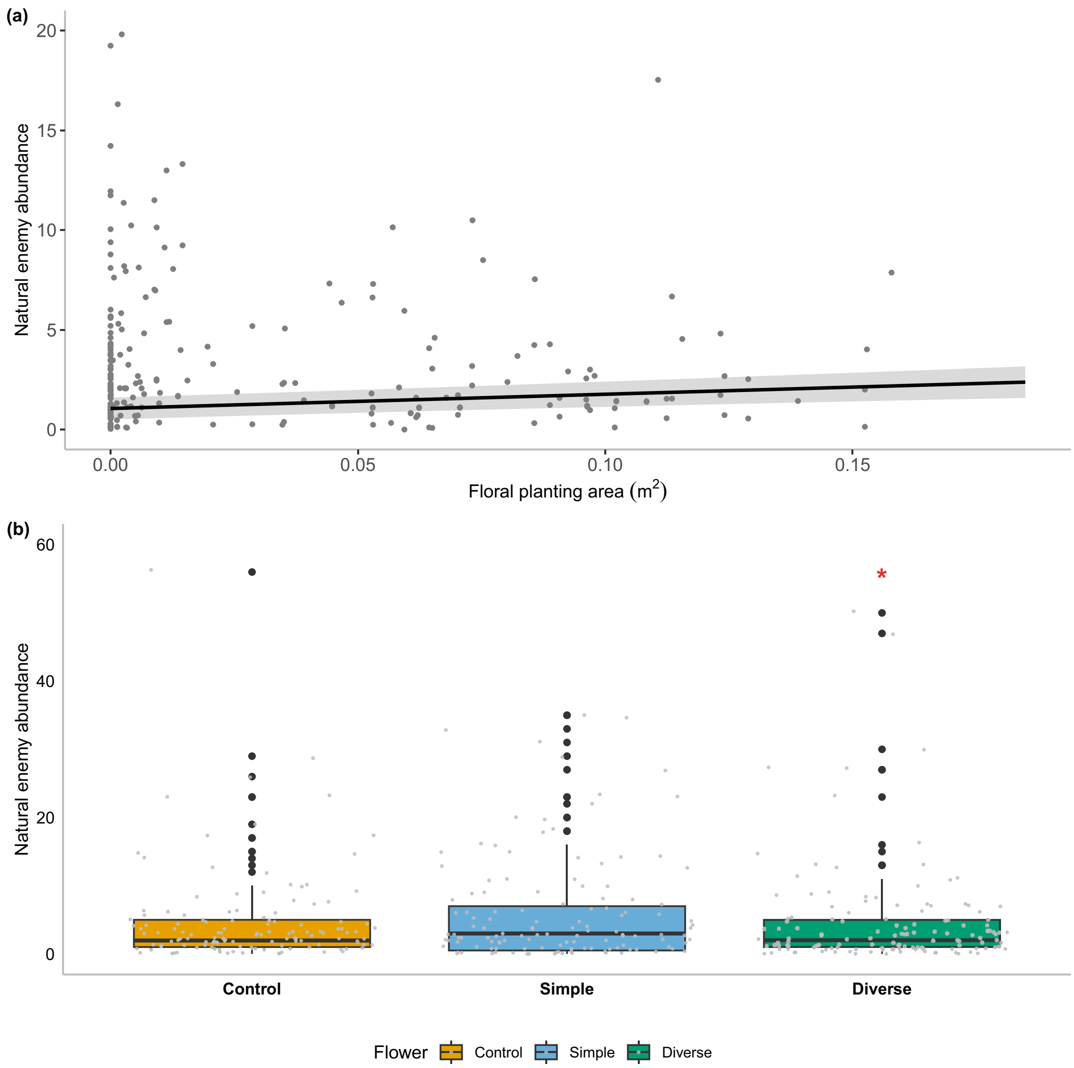

FIGURE 2 Relationship between natural enemy abundance and (a) floral area within the orchards (95% confidence interval is indicated by the shaded areas); (b) natural enemy abundance per catch and floral planting type in which the pan traps were placed (Control, Simple, Diverse). Data points are jittered for clarity. Parasitoid abundance was positively affected by an increase in floral area within the orchards (2a) but was significantly lower in diverse floral types compared to the simple planting and control 2b). The red asterix indicates significance of treatment.

Effects of habitat type on parasitoid abundance and species richness were evaluated using GLMMs with Poisson and Negative binomial error distributions. Habitat (orchard/non-crop habitat/fynbos) was included as a fixed factor, while orchard identity and sampling round were random effects. We used Post hoc Tukey tests to determine comparative differences in parasitoid abundance and species richness between habitats. The same model with a Gaussian distribution was used to test the effect of habitat type on diversity indices. We standardised continuous variables and tested for multicollinearity (VIF < 2: Graham, 2003) (Table S3).

To determine the relative influence of the environmental variables on parasitoid species abundance and composition, we performed a Canonical Correspondence Analysis (CCA). Habitat type (fynbos/inside the orchard/non-crop habitat) and landscape classes (high, medium, low levels of natural habitat) were fitted as environmental variables and a permutation test on the CCA was performed to assess their significance. Three separate analyses were run using (1) families of common species (>50 individuals overall captured in traps) with habitat type and landscape classes as constraints, (2) families of known parasitoids of apple pests (Table S4) with habitat type and landscape classes as constraints and (3) the entire parasitoid dataset within orchards with landscape classes and floral area as constraints. Model assumptions were verified by plotting residuals against fitted values and for each covariate in the model. GLMMs were performed in R (version 4.4.2) using the packages 'lme4' and 'glmmTMB' (Bates et al., 2015; Brooks et al., 2017). CCA was conducted using the 'vegan' package (Oksanen et al., 2025).

RESULTS

Overall, pan traps yielded 4278 parasitoid individuals in the 36 sampled apple orchards and orchard buffer. Several families of parasitoids were identified including Platygastroidea (49%), Chalcidoidea (28%), Eulophideae (4%), Aphelinidae (5%), Pteromalidae, Ceraphronidae and Ichneumonidae (3% each), Trichogrammatidae, Mymaridae, Bethylidae and Cynipoidea (1% each). Parasitoid abundance was positively affected by an increase in floral area within the orchards ($\beta = 6.916$, $p < 0.001$, Figure 2a; Table 2a) but was significantly lower in diverse floral types compared to the simple plantings and control (Figure 2b). We found no effect of floral planting nor of landscape class on parasitoid species richness or diversity indices (Table S5).

The non-crop habitat yielded a significantly greater abundance and species richness of parasitoids compared to the orchards and fynbos habitats (Figure 3a,b). We found the Simpson index was greater in the fynbos compared to the other habitats (Figure 3c), suggesting the occurrence of more rare species, and non-crop habitat had a significantly higher Shannon index, suggesting that the natural habitat supported more parasitoid species, but there was no evidence of species dominance (Figure 3d).

CCA with permutation test showed that assemblage structure of common parasitoids that were in the various habitats and landscape classes was significantly dissimilar to each other (Figure 4; Table S6a). When only families that contain relevant parasitoids of apple pests were included in the analysis, landscape class showed a significant dissimilarity in assemblage structure (Figure 5; Table S6b). Higher percentage of natural habitat in landscape class strongly affected the composition of the parasitoid assemblage within the orchards (Figure 6; Table S6c).

TABLE 2 Estimates (β), SE and 95% confidence intervals of the fixed effects included in the best model explaining the abundance of natural enemies in: (a) pan trap catches within the orchards (Poisson, $\Delta AIC < 2$) (b) pan trap catches across apple orchards and surrounding non-crop (negative binomial, $\Delta AIC < 2$) (c) the species richness of natural enemies across apple orchards and surrounding non-crop (negative binomial, $\Delta AIC < 2$) in the Cape Floristic Region, South Africa.

			95% confidence interval	
Variable	**ß**	**SE**	**Lower limit**	**Upper limit**
(a)				
Intercept	**1.185**	**0.312**	**0.550**	**1.806**
Floral area	**6.916**	**1.503**	**3.993**	**9.927**
Flower diverse	**−0.483**	**0.207**	**−0.901**	**−0.077**
Land500	−0.194	0.672	−1.540	1.176
Flower simple	0.307	0.168	−0.028	0.642
(b)				
Intercept	0.564	0.614	−0.639	1.768
Habitat non-crop	**1.715**	**0.624**	**0.491**	**2.938**
Habitat work row	0.862	0.620	−0.353	2.077
(c)				
Intercept	0.187	0.320	−0.440	0.814
Habitat non-crop	**0.941**	**0.314**	**0.325**	**1.556**
Habitat work row	0.521	0.311	−0.088	1.132

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

DISCUSSION

This study demonstrated that floral enhancement practices and the complexity of the surrounding landscape influenced parasitoid assemblage composition and abundance within apple orchards in the Kogelberg Biosphere Reserve in the CFR of South Africa.

Increasing floral resources through flower planting elevated the abundance of parasitoids in apple orchards, conceivably by boosting resource availability (nectar, pollen, prey, hosts) and shelter (Gurr et al., 2017), which is consistent with findings in apple orchards in other, more temperate, regions (Barda et al., 2025; Dib et al., 2012; Tougeron et al., 2023) and other perennial crops such as pear and olive (Álvarez et al., 2024; Ji et al., 2022). This finding, together with parallel findings for orchard pollinators (Ratto et al., 2021), indicates an overall positive effect of floral resources on beneficial insects, including parasitoids, in apple orchards (Fountain, 2022; Rodríguez-Gasol et al., 2019). Our findings reinforce the argument for floral enhancement management practices within a biosphere transition zone as an important element for maintaining parasitoid abundance within agricultural landscapes in the CFR.

Interestingly, parasitoid abundance was significantly lower in the diverse flower plantings compared to the simple ones, despite the former containing on average a higher percentage of floral area cover (Table S7). This may be explained by the impact of floral traits, such as an open floral structure and colour on parasitoid attraction and performance. For example, the white flowers of *L. maritima* can benefit egg parasitoid survival significantly more than other colours (Begum et al., 2004). Furthermore, *L. maritima* performs better than other plants in attracting parasitoids, by providing a nutrient-rich food source and enhancing parasitoid fitness, longevity and fecundity (Balzan & Wäckers, 2013; Chen et al., 2020; Theron et al., 2020b; Urbaneja-Bernat et al., 2024). Even though overall floral area appeared to be the best predictor of parasitoid abundance in our study, a careful selection of plant species is crucial to maximise the benefit to parasitoid fitness and longevity throughout transformed landscapes.

Parasitoid abundance, species richness and Shannon diversity were greater in the non-crop habitat adjacent to the orchards than within the orchards or in the natural fynbos matrix. This is largely in keeping with similar studies in the CFR (Gaigher et al., 2016; Theron et al., 2020b) where old fields adjacent to vineyards supported greater abundance and species richness of parasitoids and predators than inside the fields. This was due to the greater plant diversity, structural complexity and potential host/prey abundance in these semi-natural habitats. However, in contrast to our findings, these studies show that the fynbos supported greater abundance and diversity of natural enemies. It should be noted that the sampling effort in the fynbos here was substantially lower compared to the other habitats in our study. More research is needed on the effect of floral cover across natural and human-dominated habitats to provide a robust representation of the parasitoid assemblages supported in the fynbos around apple orchards.

We found that the Simpson diversity index was significantly higher in the fynbos compared to the other habitats, which aligns with

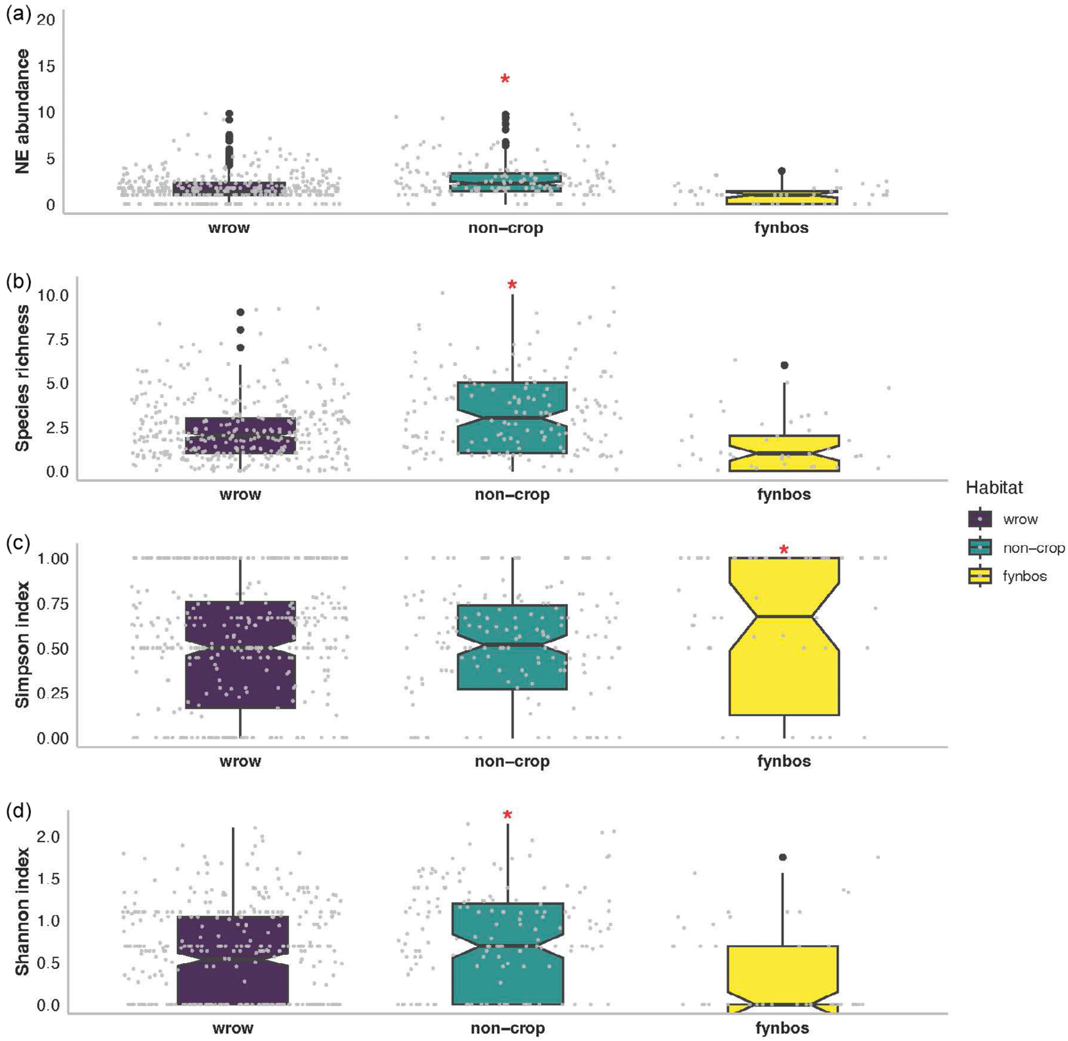

FIGURE 3 Notched boxplots showing the effect of habitat type (workrow inside the orchard, non-crop area 5 m from the orchard edge, fynbos) on natural enemy (a) Abundance; (b) Species richness; (c) Simpson index; (d) Shannon index. There was greater abundance and species richness of parasitoids in the 5 m non-crop habitat compared to the orchard and fynbos habitats (3a,b). The Simpson index was greater in the fynbos compared to the other habitats (3c), while the non-crop areas had a significantly higher Shannon index. The red asterix indicates significance of treatment.

other studies in the CFR that found highly diverse assemblages of arthropods in the fynbos (Gaigher & Samways, 2010, 2014; Kehinde & Samways, 2012). As the Simpson index accounts for evenness and dominance, our findings indicate that the fynbos supports a high number of species, but none are significantly dominant, hence supporting a relatively even distribution of individuals across species, as opposed to the non-crop and orchards which are dominated by fewer species.

The much lower abundance and species richness of parasitoids found inside the apple orchards could be due to management strategies that make highly selective use of synthetic pesticides (Witt & Samways, 2004). Growing evidence is highlighting the detrimental effect of synthetic pesticides on beneficial insects, including parasitoids (Teder & Knapp, 2019), which could negate the positive effect of resource enhancement by affecting their reproduction and survival and reducing habitat quality and availability (Ndakidemi et al., 2016; Samanta et al., 2023). However, it is not out of the question that habitat simplification, such as the active elimination of perceived competing floral resources within the orchards is also playing a role; that is, pesticides and habitat simplification are adversely synergistic. Apple tree canopy shading effects might also be contributing to reduced parasitoid levels in contrast to the situation in the naturally short sclerophyllus vegetation, as detected for endemic grasshoppers associated with apple orchards in the area (Adu-Acheampong et al., 2016).

Landscape complexity in the 500-m buffer around orchards affected species composition but not the abundance of parasitoids, which contrasts with a wealth of evidence showing the positive effect of landscape complexity on abundance, species richness and diversity of beneficial insects (Estrada-Carmona et al., 2022; Marja et al., 2022; Medeiros et al., 2019). However, small parasitoids may have reduced

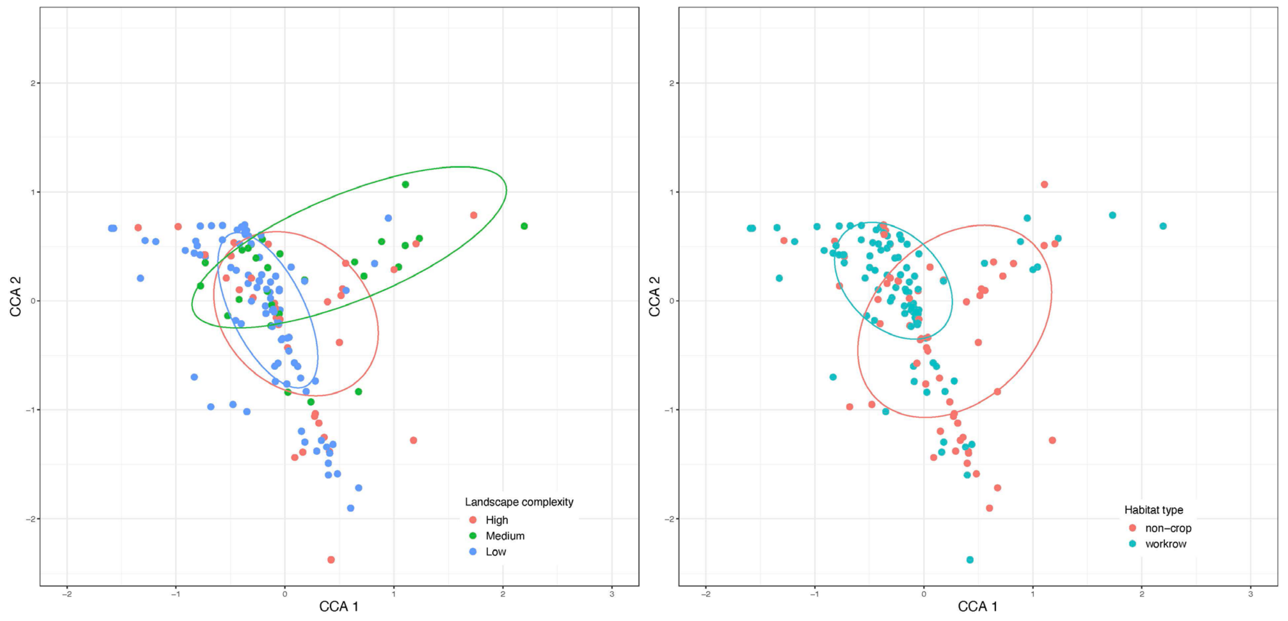

FIGURE 4 Visualisation of Canonical Correspondence Analysis (CCA) performed on the most common species of parasitoids using (a) landscape complexity and (b) habitat type as constraints in the ordination. Categorical environmental variables are represented as centroids. There was a significant effect of habitat and landscape complexity on the assemblage structure of common parasitoids.

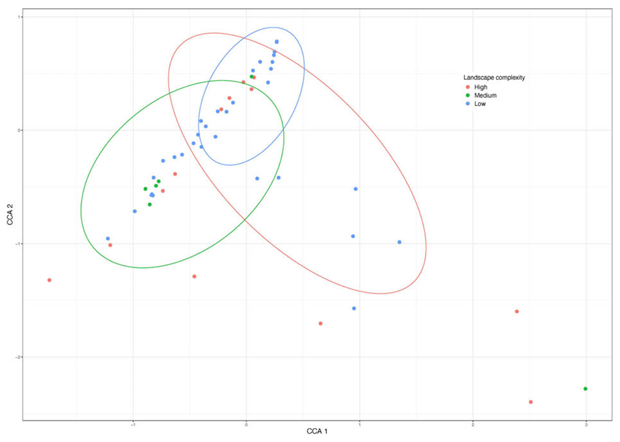

FIGURE 5 Visualisation of Canonical Correspondence Analysis (CCA) performed on families of known parasitoids of apple pests using landscape complexity as a constraint in the ordination. Categorical environmental variables are represented as centroids. Landscape complexity had a significant effect on the assemblage structure.

mobility and function at a small spatial scale, while larger natural enemies such as predators operate over intermediate spatial scales (Tscharntke et al., 2005). Furthermore, while using the percentage of non-crop habitats is a simple but robust indicator of landscape structure (Steffan-Dewenter et al., 2001, 2002; Thies & Tscharntke, 1999), more research is needed towards understanding the value to parasitoids of different landscape descriptors, including heterogeneity, configuration, connectivity and the role of different habitat types within the landscape. It is possible that the percentage of suitable habitat in the set buffer is not enough to influence parasitoids in orchards, in agreement with Gaigher et al. (2015) as they may need better connectivity and heterogeneity within a few hundred meters. Additionally, the Rosaceae do not contribute much to the fynbos flora; hence, it is conceivable that only a few apple pests may be suitable hosts for native parasitoids of the South African fynbos. Furthermore, because our study covered a relatively small geographic area, climatic variations are unlikely to have played a major role. However, future studies conducted across larger spatial scales should include environmental variables to assess whether they explain observed patterns and sources of variation. Lastly, future research should expand the geographical area and replication of landscape categories to enhance the robustness of our findings.

Although our results show that floral enhancements increased natural enemies in orchards and (semi)-natural vegetation at the farm scale supported high parasitoid diversity, there may be resistance from growers to take on the costs of planting flower plots/strips within their fields. However, Ratto et al. (2021) showed how these management practices also enhanced pollinator activity and increased apple size showing a potential gross return of circa R4 160 per ha (c. $220) attributable to floral planting. It is key that the dissemination of these results to farming communities includes the synergistic values of floral planting, with context-specific evidence and potential economic returns to encourage the uptake of these practices. Furthermore, there may be additional value over time as more species accumulate in small fragments positioned in a relatively mild (as opposed to hostile) matrix (Deane & Riva, 2025), as is the case here.

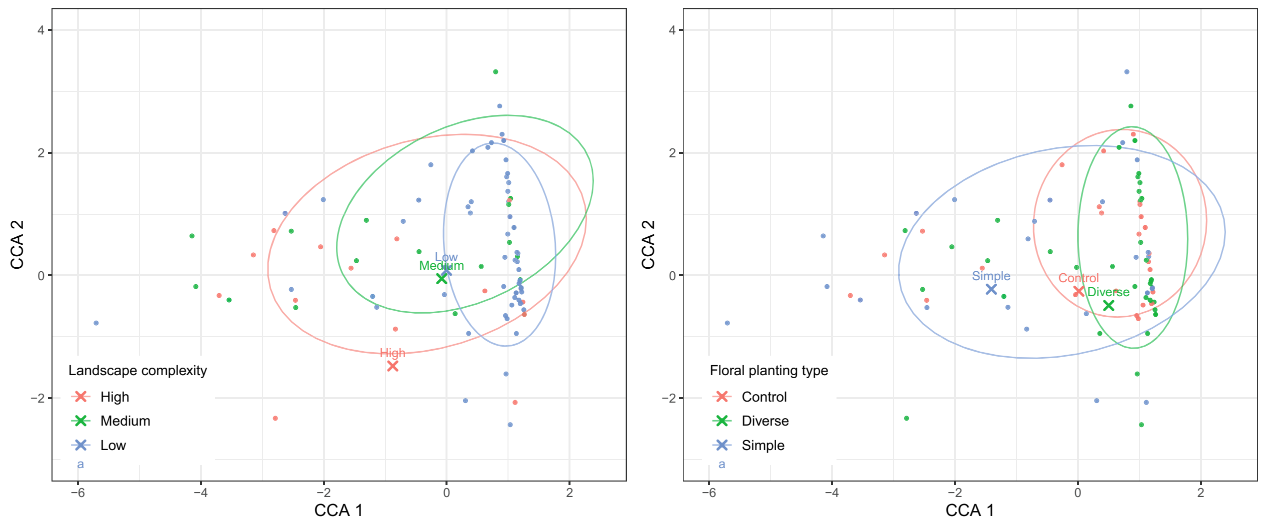

FIGURE 6 Visualisation of Canonical Correspondence Analysis (CCA) performed on parasitoids caught inside the orchards using both the categorical and continuous variables for landscape complexity as constraints in the ordination. Categorical environmental variables are represented as centroids; continuous environmental variables are represented as arrows. Landscape complexity strongly affected the composition of the parasitoid assemblage within the orchards.

CONCLUSIONS

In support of the principle of moving away from a conventional apple production to a more sustainable agroecological approach, the introduction of increased floral resources clearly improved the local diversity of parasitoids in this system. This finding is in keeping with the ethos and aims of biosphere reserves where the intention is to improve levels of biodiversity towards those that would occur in the natural areas within the buffer and transition zones, while at the same time supporting food production.

However, the details of how this comes about are complex and contingent on the ecology of the various parasitoid species and their function. Furthermore, the various levels of functional connectivity across the landscape and the differential mobility and dispersal traits of the parasitoids, which will be searching both for mates and hosts, will also affect the assemblage composition of the parasitoids. However, the results here clearly point to flower plantings as a shift in the right direction towards a more agroecological production approach, that can be refined further in the future.

AUTHOR CONTRIBUTIONS

Fabrizia Ratto: Writing – original draft; methodology; visualization; validation; writing – review and editing; formal analysis; data curation. **Peter Steward:** Investigation; methodology; writing – review and editing; data curation; validation; project administration. **Steven M. Sait:** Conceptualization; funding acquisition; methodology; writing – review and editing; supervision. **Julien M. Haran:** Methodology; writing – review and editing; formal analysis; data curation. **Rene Gaigher:** Writing – review and editing; methodology; validation. **James S. Pryke:** Conceptualization; funding acquisition; methodology; writing – review and editing; validation. **Michael J. Samways:** Conceptualization; funding acquisition; writing – review and editing; validation; methodology. **William Kunin:** Conceptualization; writing – review and editing; validation; methodology; funding acquisition; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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REFERENCES

Adu-Acheampong, S., Bazelet, C.S. & Samways, M.J. (2016) Extent to which an agricultural mosaic supports endemic species-rich grasshopper assemblages in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems and Environment*, 227, 52–60. Available from: https://doi.org/10.1016/j.agee.2016.04.019

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B. et al. (2020) Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, 57, 2170–2179. Available from: https://doi.org/10.1111/1365-2664.13712

Albrecht, M., Kleijn, D., Williams, N., Laidlaw, H.H.J., Tschumi, M., Blaauw, B. et al. (2020) Global synthesis of the effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield. *Ecology Letters*, 23(10), 1488–1498. Available from: https://doi.org/10.1111/ele.13576

Alignier, A., Solé-Senan, X.O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D. et al. (2020) Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, 57, 654–663. Available from: https://doi.org/10.1111/1365-2664.13585

Álvarez, H.A., Clemente-Orta, G. & Ruano, F. (2024) Ants and predators cope with pest pressures by interacting with the surrounding vegetation at low spatial scales. *Journal of Applied Entomology*, 148, 1187–1197. Available from: https://doi.org/10.1111/jen.13338

Balzan, M.V. & Wäckers, F.L. (2013) Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. *Biological Control*, 67, 21–31. Available from: https://doi.org/10.1016/j.biocontrol.2013.06.006

Barda, M.S., Karamaouna, F., Kati, V., Stathakis, T.I., Economou, L.P. & Perdikis, D.C. (2025) Flowering plant patches to support the conservation of natural enemies of pests in apple orchards. *Agriculture, Ecosystems and Environment*, 381, 109405. Available from: https://doi.org/10.1016/j.agee.2024.109405

Batáry, P., Báldi, A., Ekroos, J., Gallé, R., Grass, I. & Tscharntke, T. (2020) Biologia Futura: landscape perspectives on farmland biodiversity conservation. *Biologia Futura*, 71, 9–18. Available from: https://doi.org/10.1007/s42977-020-00015-7

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) lme4: Linear mixed-effects models using Eigen and S4. R Package Version, 1(1–8).

Begum, M., Gurr, G., Wratten, S. & Nicol, H. (2004) Flower color affects tri-trophic-level biocontrol interactions. *Biological Control*, 30, 584–590. Available from: https://doi.org/10.1016/J.BIOCONTROL.2004.03.005

Blaauw, B.R. & Isaacs, R. (2012) Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. *Ecological Entomology*, 37, 386–394. Available from: https://doi.org/10.1111/j.1365-2311.2012.01376.x

Botha, M., Siebert, S.J., van den Berg, J., Ellis, S. & Greyvenstein, B.M. (2018) Diversity patterns of selected predaceous arthropod groups in maize fields and margins in south African Highveld grassland. *Agricultural and Forest Entomology*, 20, 461–475. Available from: https://doi.org/10.1111/afe.12277

Botha, M., Siebert, S.J., van den Berg, J., Maliba, B.G. & Ellis, S.M. (2015) Plant and arthropod diversity patterns of maize agro-ecosystems in two grassy biomes of South Africa. *Biodiversity and Conservation*, 24, 1797–1824. Available from: https://doi.org/10.1007/s10531-015-0901-0

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) Modeling Zero-Inflated Count Data With glmmTMB. bioRxiv 132753. https://doi.org/10.1101/132753

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.

Campbell, A.J., Wilby, A., Sutton, P. & Wäckers, F.L. (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture, Ecosystems and Environment*, 239, 20–29. Available from: https://doi.org/10.1016/j.agee.2017.01.005

Chen, Y., Mao, J., Reynolds, O.L., Chen, W., He, W., You, M. et al. (2020) Alyssum (*Lobularia maritima*) selectively attracts and enhances the performance of *Cotesia vestalis*, a parasitoid of *Plutella xylostella*. *Scientific Reports*, 10, 6447. Available from: https://doi.org/10.1038/s41598-020-62021-y

Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003) A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation*, 112, 191–216. Available from: https://doi.org/10.1016/S0006-3207(02)00425-1

DEA. (2016) South African National Land Cover (SANLC) 2014 and 2018 Change Assessment Datasets. Available at: https://egis.environment.gov.za/sa_national_land_cover_datasets

Deane, D.C. & Riva, F. (2025) Time and matrix quality increase the relative habitat value of smaller patches in fragmented landscapes. *Journal of Applied Ecology*, 62, 958–969. Available from: https://doi.org/10.1111/1365-2664.14884

Dib, H., Libourel, G. & Warlop, F. (2012) Entomological and functional role of floral strips in an organic apple orchard: hymenopteran parasitoids as a case study. *Journal of Insect Conservation*, 16, 315–318. Available from: https://doi.org/10.1007/s10841-012-9471-6

Esler, K.J., Pierce, S.M. & De Villiers. C. (2014) *Fynbos ecology and management*. Pretoria: Briza Publications.

Estrada-Carmona, N., S anchez, A.C., Remans, R. & Jones, S.K. (2022) Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. https://doi.org/10.1073/pnas

Evans, E.W. (2018) Dispersal in host–parasitoid interactions: crop colonization by pests and specialist enemies. *Insects*, 9(4), 134. Available from: https://doi.org/10.3390/insects9040134

Fitzgerald, J.D. & Solomon, M.G. (2004) Can flowering plants enhance numbers of beneficial arthropods in UK apple and pear orchards? *Biocontrol Science and Technology*, 14, 291–300. Available from: https://doi.org/10.1080/09583150410001665178

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M. et al. (2011) Solutions for a cultivated planet. *Nature*, 478, 337–342. Available from: https://doi.org/10.1038/nature10452

Fountain, M.T. (2022) Impacts of wildflower interventions on beneficial insects in fruit crops: a review. *Insects*, 13, 304. Available from: https://doi.org/10.3390/insects13030304

Gaigher, R., Pryke, J.S., Kratschmer, S., Zaller, J.G., Winter, S., Samways, M.J. et al. (2024) Area and configuration of both semi-natural habitats and vineyards influence arthropods in south African and central European agricultural landscapes. *Insect Conservation and Diversity*, 17, 702–718. Available from: https://doi.org/10.1111/icad.12741

Gaigher, R., Pryke, J.S. & Samways, M.J. (2015) High parasitoid diversity in remnant natural vegetation, but limited spillover into the agricultural matrix in south African vineyard agroecosystems. *Biological Conservation*, 186, 69–74. Available from: https://doi.org/10.1016/j.biocon.2015.03.003

Gaigher, R., Pryke, J.S. & Samways, M.J. (2016) Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. *Agriculture, Ecosystems and Environment*, 230, 242–250. Available from: https://doi.org/10.1016/j.agee.2016.06.014

Gaigher, R. & Samways, M.J. (2010) Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. *Journal of Insect Conservation*, 14, 595–605. Available from: https://doi.org/10.1007/s10841-010-9286-2

Gaigher, R. & Samways, M.J. (2014) Landscape mosaic attributes for maintaining groundliving spider diversity in a biodiversity hotspot. *Insect Conservation and Diversity*, 7, 470–479. Available from: https://doi.org/10.1111/icad.12070

Gaigher, R., van den Berg, J., Batáry, P. & Grass, I. (2024) Agroecological farming for insect conservation. In: Pryke, J.S., Samways, M.J., New, T.R., Cardoso, P. & Gaigher, R. (Eds.) *Routledge handbook of insect conservation*, 1st edition. London: Routledge.

Galan, M., Pons, J.B., Tournayre, O., Pierre, É., Leuchtmann, M., Pontier, D. et al. (2018) Metabarcoding for the parallel identification of several hundred predators and their prey: application to bat species diet analysis. *Molecular Ecology Resources*, 18, 474–489. Available from: https://doi.org/10.1111/1755-0998.12749

Galloway, A.D., Seymour, C.L., Gaigher, R. & Pryke, J.S. (2021) Organic farming promotes arthropod predators, but this depends on neighbouring patches of natural vegetation. *Agriculture, Ecosystems and Environment*, 310, 107295. Available from: https://doi.org/10.1016/j.agee.2020.107295

García, R.R. & Miñarro, M. (2014) Role of floral resources in the conservation of pollinator communities in cider-apple orchards. *Agriculture, Ecosystems & Environment*, 183, 118–126. Available from: https://doi.org/10.1016/j.agee.2013.10.017

Geldenhuys, M., Gaigher, R., Pryke, J.S. & Samways, M.J. (2021) Diverse herbaceous cover crops promote vineyard arthropod diversity across different management regimes. *Agriculture, Ecosystems and Environment*, 307, 107222. Available from: https://doi.org/10.1016/j.agee.2020.107222

Geldenhuys, M., Gaigher, R., Pryke, J.S. & Samways, M.J. (2022a) Interplay between amount of natural vegetation and effective vineyard management practices benefits local arthropod diversity. *Biodiversity and Conservation*, 31, 3039–3053. Available from: https://doi.org/10.1007/s10531-022-02473-y

Geldenhuys, M., Gaigher, R., Pryke, J.S. & Samways, M.J. (2022b) Vineyards compared to natural vegetation maintain high arthropod species turnover but alter trait diversity and composition of assemblages. *Agriculture, Ecosystems and Environment*, 336, 108043. Available from: https://doi.org/10.1016/j.agee.2022.108043

Geldenhuys, M., Gaigher, R., Pryke, J.S. & Samways, M.J. (2022c) Maintaining remnant vegetation along with plant diversification in vineyards is optimal for conserving arthropods in an agricultural mosaic in a biodiversity-rich region. *Biodiversity and Conservation*, 31, 3237–3255. Available from: https://doi.org/10.1007/s10531-022-02486-7

Goldblatt, P. & Manning, J.C. (2000) The long-proboscid fly pollination system in southern Africa. *Annals of the Missouri Botanical Garden*, 87, 146–170. Available from: https://doi.org/10.2307/2666158

Gomez, J.M. (2000) Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. *Oecologia*, 122, 90–97. Available from: https://doi.org/10.1007/PL00008840

Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, 84(11), 2809–2815.

Grant, P.B.C. & Samways, M.J. (2011) Micro-hotspot determination and buffer zone value for Odonata in a globally significant biosphere reserve. *Biological Conservation*, 144(2), 772–781. Available from: https://doi.org/10.1016/j.biocon.2010.11.008

Greeff, P. & Kotze, M. (2007) *Subsector study: deciduous fruits*. Pretoria, South Africa: National Agricultural Marketing Council.

Gurr, G.M., Wratten, S.D., Landis, D.A. & You, M. (2017) Habitat management to suppress Pest populations: Progress and prospects. *Annual Review of Entomology*, 62, 91–109. Available from: https://doi.org/10.1146/annurev-ento-031616-035050

Habel, J.C., Samways, M.J. & Schmitt, T. (2019) Mitigating the precipitous decline of terrestrial European insects: requirements for a new strategy. *Biodiversity and Conservation*, 28, 1343–1360. Available from: https://doi.org/10.1007/s10531-019-01741-8

Henri, D.C., Jones, O., Tsiattalos, A., Thébault, E., Seymour, C.L. & van Veen, F.J.F. (2015) Natural vegetation benefits synergistic control of the three main insect and pathogen pests of a fruit crop in southern Africa. *Journal of Applied Ecology*, 52, 1092–1101. Available from: https://doi.org/10.1111/1365-2664.12465

Janion-Scheepers, C., Bengtsson, J., Duffy, G.A., Deharveng, L., Leinaas, H.P. & Chown, S.L. (2020) High spatial turnover in springtails of the Cape Floristic Region. *Journal of Biogeography*, 47, 1007–1018. Available from: https://doi.org/10.1111/jbi.13801

Ji, X.Y., Wang, J.Y., Dainese, M., Zhang, H., Chen, Y.J., Cavalieri, A. et al. (2022) Ground cover vegetation promotes biological control and yield in pear orchards. *Journal of Applied Entomology*, 146(3), 262–271. Available from: https://doi.org/10.1111/jen.12965

Johns, A. & Johns, M. (2001) *Kogelberg biosphere reserve : heart of the cape flora*. Cape Town, South Africa: Struik.

Kehinde, T. & Samways, M.J. (2012) Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, Ecosystems and Environment*, 146, 162–167. Available from: https://doi.org/10.1016/j.agee.2011.10.020

Kehinde, T. & Samways, M.J. (2014) Insect-flower interactions: network structure in organic versus conventional vineyards. *Animal Conservation*, 17, 401–409. Available from: https://doi.org/10.1111/acv.12118

Kemp, J.E. & Ellis, A.G. (2017) Significant local-scale plant-insect species richness relationship independent of abiotic effects in the temperate cape floristic region biodiversity hotspot. *PLoS One*, 12, e0168033. Available from: https://doi.org/10.1371/journal.pone.0168033

Kozich, J.J., Westcott, S.L., Baxter, N.T., Highlander, S.K. & Schloss, P.D. (2013) Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the miseq illumina sequencing platform. *Applied and Environmental Microbiology*, 79, 5112–5120. Available from: https://doi.org/10.1128/AEM.01043-13

Lérault, L., Clavel, E., Villegas, C.M., Cabrera, N., Jaloux, B., Plantegenest, M. et al. (2022) Providing alternative hosts and nectar to aphid parasitoids in a plum orchard to determine resource complementarity and distance range effect on biological control. *Agronomy*, 12(1), 77. Available from: https://doi.org/10.3390/agronomy12010077

Marja, R., Tscharntke, T. & Batáry, P. (2022) Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – a meta-analysis. *Agriculture, Ecosystems and Environment*, 326, 107822. Available from: https://doi.org/10.1016/j.agee.2021.107822

Medeiros, H.R., Martello, F., Almeida, E.A.B., Mengual, X., Harper, K.A., Grandinete, Y.C. et al. (2019) Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes. *Biological Conservation*, 238, 108193. Available from: https://doi.org/10.1016/j.biocon.2019.07.038

Ndakidemi, B., Mtei, K. & Ndakidemi, P.A. (2016) Impacts of synthetic and botanical pesticides on beneficial insects. *Agricultural Sciences*, 07, 364–372. Available from: https://doi.org/10.4236/as.2016.76038

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P. et al. (2025) "vegan: Community Ecology Package.". R Package Version, 2.6–10.

Penel, B., Meynard, C.N., Benoit, L., Boudonne, A., Clamens, A.L., Soldati, L. et al. (2025) The best of two worlds: toward large-scale monitoring of biodiversity combining COI metabarcoding and optimized parataxonomic validation. *Ecography* 6, 1–13. Available from: https://doi.org/10.1111/ecog.07699

Pool-Stanvliet, R., Stoll-Kleemann, S. & Giliomee, J.H. (2018) Criteria for selection and evaluation of biosphere reserves in support of the UNESCO MAB programme in South Africa. *Land Use Policy*, 76, 654–663. Available from: https://doi.org/10.1016/j.landusepol.2018.02.047

Procheş, Ş. & Cowling, R.M. (2006) Insect diversity in *Cape fynbos* and neighbouring south African vegetation. *Global Ecology and Biogeography*, 15, 445–451. Available from: https://doi.org/10.1111/j.1466-822X.2006.00239.x

Ratto, F., Steward, P., Sait, S.M., Pryke, J.S., Gaigher, R., Samways, M.J. et al. (2021) Proximity to natural habitat and flower plantings increases insect populations and pollination services in south African apple orchards. *Journal of Applied Ecology*, 58, 2540–2551. Available from: https://doi.org/10.1111/1365-2664.13984

Rodríguez-Gasol, N., Avilla, J., Aparicio, Y., Arnó, J., Gabarra, R., Riudavets, J. et al. (2019) The contribution of surrounding margins in the promotion of natural enemies in mediterranean apple orchards. *Insects*, 10, 148. Available from: https://doi.org/10.3390/insects10050148

Rouget, M., Richardson, D.M. & Cowling, R.M. (2003) The current configuration of protected areas in the cape floristic region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biological Conservation*, 112, 129–145. Available from: https://doi.org/10.1016/S0006-3207(02)00396-8

Samanta, S., Maji, A., Sutradhar, B., Banerjee, S., Shelar, V.B., Khaire, P.B. et al. (2023) Impact of pesticides on beneficial insects in various agroecosystem: a review. *International Journal of Environment and Climate Change*, 13, 1928–1936. Available from: https://doi.org/10.9734/ijecc/2023/v13i82149

Samways, M.J., Pryke, J.S., Gaigher, R. & Deacon, C. (2024a) Biosphere reserves in the megadiverse Cape Floristic Region are effective in conserving arthropod diversity. *Integrative Conservation*, 3, 312–329. Available from: https://doi.org/10.1002/inc3.72

Samways, M.J., Pryke, J.S., Gaigher, R. & Deacon, C. (2024b) Eco-evolutionary origins and diversification in a megadiverse hotspot: arthropods in the greater cape floristic region. *Ecology and Evolution*, 14, e70195. Available from: https://doi.org/10.1002/ece3.70195

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. et al. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters*, 16, 912–920. Available from: https://doi.org/10.1111/ele.12128

Shannon, C.E. (1948) A mathematical theory of communication. *The Bell System Technical Journal*. 27, 379–423.

Shweta, M. & Rajmohana, K. (2018) A comparison of sweep net, yellow pan trap and malaise trap for sampling parasitic hymenoptera in a backyard habitat in Kerala. *Entomon*, 43(1), 33–44.

Simpson, E.H. (1949) Measurement of diversity. *Nature*, 163, 688.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A. et al. (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 16442–16447. Available from: https://doi.org/10.1073/pnas.1906419116

Sow, A., Brévault, T., Delvare, G., Haran, J., Benoit, L., Cœur d'Acier, A. et al. (2018) DNA sequencing to help identify crop pests and their natural enemies in agro-ecosystems: the case of the millet head miner *Heliocheilus albipunctella* (Lepidoptera: Noctuidae) in sub-Saharan Africa. *Biological Control*, 121, 199–207. Available from: https://doi.org/10.1016/j.biocontrol.2018.03.007

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432. Available from: https://doi.org/10.2307/3071954

Steffan-Dewenter, I., Münzenberg, U. & Tscharntke, T. (2001) Pollination, seed set and seed predation on a landscape scale. *Proceedings. Biological Sciences/The Royal Society*, 268, 1685–1690. Available from: https://doi.org/10.1098/rspb.2001.1737

Steward, P.R., Shackelford, G., Carvalheiro, L.G., Benton, T.G., Garibaldi, L.A. & Sait, S.M. (2014) Pollination and biological control research: are we neglecting two billion smallholders. *Agriculture & Food Security*, 3, 5. Available from: https://doi.org/10.1186/2048-7010-3-5

Teder, T. & Knapp, M. (2019) Sublethal effects enhance detrimental impact of insecticides on non-target organisms: a quantitative synthesis in parasitoids. *Chemosphere*, 214, 371–378. Available from: https://doi.org/10.1016/j.chemosphere.2018.09.132

Theron, K.J., Gaigher, R., Pryke, J.S. & Samways, M.J. (2020a) High quality remnant patches in a complex agricultural landscape sustain high spider diversity. *Biological Conservation*, 243, 108480. Available from: https://doi.org/10.1016/j.biocon.2020.108480

Theron, K.J., Gaigher, R., Pryke, J.S. & Samways, M.J. (2020b) Abandoned fields and high plant diversity support high spider diversity within an agricultural mosaic in a biodiversity hotspot. *Biodiversity and Conservation*, 29, 3757–3782. Available from: https://doi.org/10.1007/s10531-020-02048-9

Thies, C. & Tscharntke, T. (1999) Landscape structure and biological control in agroecosystems. *Science*, 285(5429), 893–895.

Tougeron, K., Ferrais, L., Gardin, P., Lateur, M. & Hance, T. (2023) Flower strips increase the control of rosy apple aphids after parasitoid releases in an apple orchard. *Annals of Applied Biology*, 182(2), 245–256. Available from: https://doi.org/10.1111/aab.12816

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, 8, 857–874. Available from: https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P. et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87, 661–685. Available from: https://doi.org/10.1111/j.1469-185X.2011.00216.x

Urbaneja-Bernat, P., Riudavets, J., Denis, C., Ojeda, J., Alomar, O. & Arnó, J. (2024) *Lobularia maritima* as a nutrient-rich floral food source for two parasitoid wasps of *Tuta absoluta*. *Entomologia Generalis*, 44, 339–346. Available from: https://doi.org/10.1127/entomologia/2024/2299

van Schalkwyk, J., Pryke, J.S., Samways, M.J. & Gaigher, R. (2019) Complementary and protection value of a Biosphere Reserve buffer zone for increasing local representativeness of ground-living arthropods. *Biological Conservation*, 239, 108292. Available from: https://doi.org/10.1016/j.biocon.2019.108292

WCDA. (2017) CapeFarmMapper 2.0.5 User manual. Available at: https://gis.elsenburg.com/apps/cfm/docs/CapeFarmMapper%202.0.5%20User%20Manual.pdf

Wilson, J.S., Jahner, J.P., Starley, L., Calvin, C.L., Ikerd, H. & Griswold, T. (2016) Sampling bee communities using pan traps: alternative methods increase sample size. *Journal of Insect Conservation*, 20, 919–922. Available from: https://doi.org/10.1007/s10841-016-9914-6

Winter, S., Bauer, T., Strauss, P., Kratschmer, S., Paredes, D., Popescu, D. et al. (2018) Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: a meta-analysis. *Journal of Applied Ecology*, 55, 2484–2495. Available from: https://doi.org/10.1111/1365-2664.13124

Witt, A.B.R. & Samways, M.J. (2004) Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology*, 12, 89–95.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Land cover classes with code and descriptions, used in the analysis (South African National Land Cover (SANLC) https://gee-community-catalogue.org/projects/sa_nlc/).

Table S2. List of species planted in the experimental floral plots in both the 'diverse' and 'simple' plot treatments.

Table S3. Outputs for multicollinearity test amongst factors used in the linear models.

Table S4 List of known parasitoids of apple pests (Thorpe, Pryke and Samways, 2016).

Table S4. Estimates (β), SE and 95% confidence intervals of the fixed effects included in the LMM, explaining (a) Species richness of natural enemies in pan trap catches within the orchards, (b) Simpson index of natural enemies in pan trap catches within the orchards and (c) Shannon richness of natural enemies in pan trap catches within the orchards.

Table S5. CCA permutation test output for (a) most common parasitoid species, (b) known parasitoids of apple pests and (c) parasitoids caught in pan traps inside the orchards.

Table S6. Average floral area per farm, divided by treatment: diverse (11 plant species), Simple (1 species planted) and Control (no species planted).

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