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Wildflower strips enhance pest regulation services in citrus orchards

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ABSTRACT

Contemporary approaches to agriculture must be reimaged to include ecological techniques that maximise ecosystem services, so that food can be produced sustainably whilst simultaneously meeting yield demands. Pest regulation services, harnessed through the conservation of natural enemies in the agri-environment are an economically important service degraded by conventional citrus production practices. For the first time, a sown wildflower strip composed of native forbs and tussock-forming grasses has been investigated for its influence on natural enemies and their pest regulation services in citrus orchards. A novel management strategy was applied, using the predicted generation times of *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), a key pest in citrus, to determine whether cutting the wildflower strips could force spill-over of natural enemies onto the adjacent crop, enhancing pest regulation services. Three treatments applied to orange orchard alleyways were compared: i) a control treatment, the standard orchard practice of regular cutting to 5 cm throughout the year, ii) a sown wildflower treatment managed with cutting once a year in February to a height of 10 cm (standard management wildflower treatment, SMWT), and iii) the same sown wildflower treatment but managed with two additional cuts in May and June (active management wildflower treatment, AMWT). Orange tree canopies were sampled for natural enemies, and pest regulation services were quantified using sentinel prey cards baited with *Ephestia kuehniella* eggs. Natural enemy richness was greatest in canopies with SMWT, supporting a greater relative abundance of primary parasitoids and lower relative abundances of antagonists (ants) compared to the control. This was associated with enhanced pest regulation services (depletion of sentinel prey from baited cards), especially during the early summer months, which coincides with a critical period to control *A. aurantii* and other key citrus pests. In contrast, AMWT did not enhance natural enemy richness, and pest regulation services were diminished. This study suggests that leaving wildflower strips uncut throughout the season, as in SMWT, may help to mitigate pest incidence through enhanced pest regulation services. Further studies are now required to determine how this would influence populations of target pests.

1. Introduction

The citrus industry is of global economic importance (Talon et al., 2020). Cultivated throughout the tropics and subtropics, the fruit are exported worldwide both for fresh and processed markets (FAO, 2021). As a perennial cropping system, citrus has the potential to support a great diversity of natural enemies, which can contribute to the natural regulation of crop pests (Urbaneja et al., 2020). Nevertheless, there are still pest species that escape satisfactory management (Urbaneja et al., 2023), and due to the global citrus trade and shifting regional climates, the risk of future invasions are accelerated and many of these pests are now of global concern, hence pesticide dependency in citrus crops is common (Urbaneja et al., 2023). Furthermore, barriers to the widespread uptake of more sustainable approaches, including the use of conservation biological control and the provision of habitat management, are prevalent (Calatrava et al., 2021). However, the value of such conservation practices to citrus industry in Florida, USA is estimated at \$1150 to \$2000 (USD) per hectare (Monzó and Stansly, 2020). Hence, this should be a great incentive to develop more sustainable and successful strategies for citrus crops.

Spain is the largest global exporter of citrus and the largest growing region in the Mediterranean basin (FAO, 2021), with Andalucía in the

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southwest now an important region for large-scale production (Massot, 2016). Over half of the total land area of Andalucia is under agriculture, shifting from small holder farms to large scale production (Massot, 2016). Such intensive anthropogenic landscapes have constrained space for semi-natural habitats (Tscharntke et al., 2012), which has come at a great cost to biodiversity (Dirzo et al., 2014; Sánchez-Bayo and Wyckhuys, 2019; Tilman, 1999). In turn, the processes which support and regulate ecosystems and the delivery of ecosystem services are undermined (Cardinale et al., 2012; Oliver et al., 2015; Scherber et al., 2010), which has been exacerbated by the ever-increasing inputs to mitigate their loss (Matson et al., 1997). The combined pressure of land use change and management has left little resource available to support natural enemies within the cropped environment, resulting in lower abundance and diversity, delayed colonisation, and reduced fitness, ultimately leading to diminished pest regulation services (Rusch et al., 2016).

To support natural enemies and reduce reliance on plant protection products, habitat creation and management approaches have been developed to maximise natural enemy fitness and enhance pest regulation services (Landis et al., 2000). Creating wildflower strips at field boundaries or in alleyways between rows of crop plants has successfully increased natural enemy abundance in fruit crops such as cherry, apple, and blueberry, and can help contribute to pest regulation services (Albrecht et al., 2020; Mateos-Fierro et al., 2021; Whitehouse et al., 2018). However, such strategies must be tailored for different climates and pests (Bischoff et al., 2022). In Mediterranean biomes, habitat interventions can increase natural enemy diversity and/or abundance in grape (Rosas-Ramos et al., 2019), pear (de Pedro et al., 2020), apple (Santos et al., 2018), olive (Carpio et al., 2019), lemon (Silva et al., 2010) and pomegranate (Kishinevsky et al., 2017) orchard systems. However, most of these studies have focused on i) preserving naturally occurring vegetation, which results in site-specific responses (Gómez-Marco et al., 2016); ii) annual and biennial flower strips, which are costly to re-sow and leads to differences in year-on-year resource availability (Fiedler and Landis, 2007); or iii) agricultural varieties, which may be poorly adapted to the local climate and provide limited support for native natural enemies (Fox and Eisenbach, 1992). However, there is limited research on the value of habitat interventions in citrus (see Monzó et al. 2020). To support the ecological intensification of these systems, further research is urgently required.

Globally, citrus orchards are most typically maintained with bare soil, with vegetation either mechanically or chemically removed both under the trees and in the alleyways between rows (Monzó et al., 2020). However, over the past decade, there has been an increase in the use of sown *Schedonorus arundinaceus* (Schreb.) grass strips in Spain (Monzó et al., 2020), predominantly for the regulation of mites and thrips through the provision of pollen and alternative prey (Aguilar-Fenollosa et al., 2011; Aguilar-Fenollosa and Jacas, 2013). Additionally, tussock-forming grasses, such as *S. arundinaceus,* provide favourable microclimates for natural enemies during weather extremes (Collins et al., 2003; Luff, 1965). However, when naturally occurring forb species establish in these grass strips, aphid management is enhanced due to the increase in floral resources (Gómez-Marco et al., 2016). By relying on species present in the vicinity, site specific responses can limit the benefits achieved, however, this can be overcome through the inclusion of wildflower species (forbs) in seed mixes used to establish alleyway habitats (Mockford et al., 2023).

By increasing the number and diversity of forbs present, the flowering period within the strips can also be extended (Mockford et al., 2023), which can then increase the breadth of plant morphological traits, supporting a greater diversity of natural enemies (Fiedler and Landis, 2007; Wäckers and van Rijn, 2012). The sowing of native perennial forbs and grasses helps provide consistent year on year resources for natural enemies, whilst reducing costs associated with using annual seed mixes (sown yearly), and irrigation to support non-native plant species not adapted to site conditions (Fiedler and Landis, 2007). There is therefore a strong rationale for creating wildflower strips that include a diversity of perennial forb species and tussock-forming grasses to support natural enemies and their pest regulation services.

Despite their demonstrated benefits in other orchard systems (Mateos-Fierro et al., 2023; McKerchar et al., 2020), the use of perennial wildflower strips as a tool to enhance pest regulation service delivery in citrus crops has not been investigated. Moreover, the potential for using cutting as a tool to encourage the movement of natural enemies from the alleyways to the adjacent crop (forced spill-over), thereby boosting pest regulation ahead of pest critical periods, has not been fully explored (Gurr et al., 2017). Goller et al. (1997) observed an increased abundance of Coccinellids in hops two weeks after cutting a leguminous strip, which was attributed to forced spill-over. In contrast, Vercher et al. (2012) did not observe forced spill-over of economically important parasitoids, including *Aphytis* (Hymenoptera: Aphelinidae), *Metaphycus*, and *Microterys* (Hymenoptera: Encyrtidae), and predators, such as *Propylea quatuordecimpunctata* and *Scymnus interruptus* (Coleoptera: Coccinellidae) from alleyways to lemon crops, following cutting of the alleway vegetation. Forced spill-over is therefore likely to depend on the composition of the alleyway vegetation and the invertebrate community present. For example, sward structure and its associated plant species diversity significantly affect arthropod community composition (Campbell et al., 2017; Fiedler and Landis, 2007). Consequently, a species-rich perennial wildflower strip designed to support natural enemies might be expected to increase spill-over following cutting.

In this study, native perennial wildflower strips described by Mockford et al. (2023) were managed with two different cutting regimes (treatments) and compared against the standard orchard management (control). The key aim was to investigate whether creating and managing perennial wildflower strips can support natural enemies in the cropped area and deliver enhanced pest regulation services in citrus. To test the principle of forced spill-over of natural enemies onto the crop, the alleyways were cut to coincide with the predicted increase in susceptible instars of *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), a key pest in citrus (Urbaneja et al., 2020). The overall aims of this study were to determine whether the creation of wildflower strips and their subsequent management could i) increase natural enemy richness and abundance, ii) influence the arthropod functional composition, and iii) enhance pest regulation services in the crop canopy.

2. Material and methods

2.1. Site description

The study was conducted in three large (>300 ha) commercial Naval orange orchards (sites), Madre del Agua, La Calvilla and Montepinos, in two different localities in the province of Huelva, south-west Andalucía (Appendix A.1). In Andalucía, agri-environmental schemes for 'Integrated Production' promote naturally occurring vegetation on the orchard floor to mitigate soil erosion (Anonymous, 2002). As such, across all study sites, naturally occurring vegetation was present in the alleyways, managed using the standard practice of cutting four to five times annually to a height of ≤5 cm, with the cuttings left *in situ*. Herbicides were applied directly under the orange trees by growers as a prophylactic measure to regulate pest species (Llorens Climet and Martín Gil, 2014) and the crop was treated with insecticides and acaricides under IPM guidelines (MAGRAMA, 2014) (Appendix A.2).

2.2. Study design

A complete randomised block design was established at four sites, each containing three different treatment plots. One experimental site was established each in orchards La Calvilla and Madre del Agua and two experimental sites were established at orchard Montepinos. The two replicate blocks at Montepinos were separated by 260 m. Treatment plots were randomly allocated within each site. Each treatment plot was

Table 1
Flowering period of species included in the seed mix. Combined flowering period was designed to extend throughout the length of the year. These species are more commonly known as [1]Yarrow, [2]Bugloss, [3]Chicory, [4]Common shrubby everlasting, [5]St John's wort, [6]White hore-hound, [7]Apple mint, [8]Yellow restharrow, [9]Ribwort plantain, [10]Arabian pea, [12]Wild clary, [12]Tansy, [13]Orchard grass, and [14]Tall fescue.

Species	Family	Flowering period												Sowing rate (%)
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Achillea millefolium[1]	Asteraceae					🟨	🟨	🟨						8.58
Anchusa azurea[2]	Boraginaceae			🟨	🟨	🟨	🟨							1.12
Cichorium intybus[3]	Asteraceae					🟨	🟨	🟨						14.64
Helichrysum stoechas[4]	Asteraceae				🟨	🟨	🟨	🟨						8.29
Hypericum perforatum[5]	Hypericaceae					🟨	🟨	🟨	🟨					6.11
Marrubium vulgare[6]	Lamiaceae		🟨	🟨	🟨	🟨	🟨	🟨	🟨					8.29
Mentha suaveolens[7]	Lamiaceae						🟨	🟨	🟨					7.35
Ononis natrix[8]	Fabaceae				🟨	🟨	🟨	🟨						8.23
Plantago lanceolata[9]	Plantaginaceae			🟨	🟨	🟨	🟨	🟨	🟨	🟨				8.23
Psoralea bituminosa[10]	Fabaceae				🟨	🟨	🟨	🟨						2.47
Salvia verbenaca[11]	Lamiaceae	🟨	🟨	🟨	🟨	🟨								1.53
Tanacetum vulgare[12]	Asteraceae							🟨	🟨	🟨				8.58
Dactylis glomerata[13]	Poaceae					🟨								8.29
Schedonorus arundinaceus [14]	Poaceae					🟨	🟨							8.29
Total		🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨				100

0.5 ha and separated from one another by at least 150 m to help ensure independence (Ries et al., 2004). The treatments investigated were i) a control treatment in which the naturally occurring vegetation in alleyways was managed conventionally by cutting to $\leq$ 5 cm four or five times throughout the year, ii) novel wildflower strips sown in alternate alleyways between rows of orange trees, managed by cutting to $\approx$ 10 cm once annually in February (hereafter Standard Management Wildflower Treatment; SMWT), and iii) novel wildflower strips sown with the same seed mix as with SMWT, but managed actively by cutting three times per year ($\approx$ 10 cm) (hereafter Active Management Wildflower Treatment; AMWT) (Appendix A.2). AMWT was timed to coincide with a forecasted peak population of a key pest, California red scale, *A. aurantii*, and aimed to force spill-over of natural enemies into the crop. First and second generations of *A. aurantii* were forecast by applying the phenology model developed by Grout et al. (1989) to climate data collected from a meteorological station at the farm La Calvilla (Gibraleón-Manzorrales), Huelva, Spain) and male flight data obtained from one of the farms. The wildflower strips were sown in alternate alleyways between rows of trees to avoid disturbance associated with orchard operations, such as pruning and maceration of the resulting material. The novel seed mix used for both wildflower treatments consisted of twelve forb species and two tussock-forming grass species that were selected to provide floral diversity across the year (Table 1), microclimate, alternative prey and hosts, pollen, and sugars (nectar and honeydew) (see Mockford et al. (2022), (2023) for details).

During the establishment year (year one), all wildflower strips, irrespective of treatment, were managed with regular cutting to a height of approximately 10 cm to promote successful establishment. In subsequent years (years two and three), the different management treatments (SMWT and AMWT) were applied. Further details of species performance are presented in Mockford et al. (2023). In year three, the orange variety was changed at Montepinos (site MTP2) in one treatment plot and so the whole block was discounted in the final year of study.

2.3. *Arthropod sampling*

Samples were collected every four weeks from May to October in year one and from April to October in years two and three. Each of the three treatment plots within a block was sampled in a day and the sampling order was randomised for each visit. To investigate the response of natural enemies to AMWT, alleyways under this treatment regime were cut 3–5 days prior to sampling.

To reduce edge effects, the outermost alleyways within the 0.5 ha plots were excluded from sampling and a 20 m buffer region was established at either end of the alleyways. As such, a 60 m-long central sampling area consisting of two alleyways between four rows of orange trees was established (Fig. 1) (Englund and Cooper, 2003). Sixteen orange trees, paired across the alleyway, were randomly selected at the start of the study, marked and sampled for the three-year duration (Fig. 1). Arthropods were randomly sampled from the orange tree canopies facing the wildflower strips using a vacuum sampler adapted from a commercial leaf-blower (Stihl BG 86 C-E) and modified for sampling arthropods on foliage. The modification consisted of an extension to the input vent tube, which increased the aperture to a diameter of 21 cm (Tena et al., 2008). A wire mesh prevented leaves and twigs from entering the sample bag. Foliage in the tree canopies was vacuumed to a height of 2 m with four suctions, each for ten seconds, per tree. Suctions from a set of paired trees were combined into one sample, so that each sample consisted of 80 seconds of suctioning. Eight samples were taken per treatment plot at each sampling date. Samples were placed on ice in the field and returned to the laboratory where they were stored frozen until identification, then in ethanol for reference.

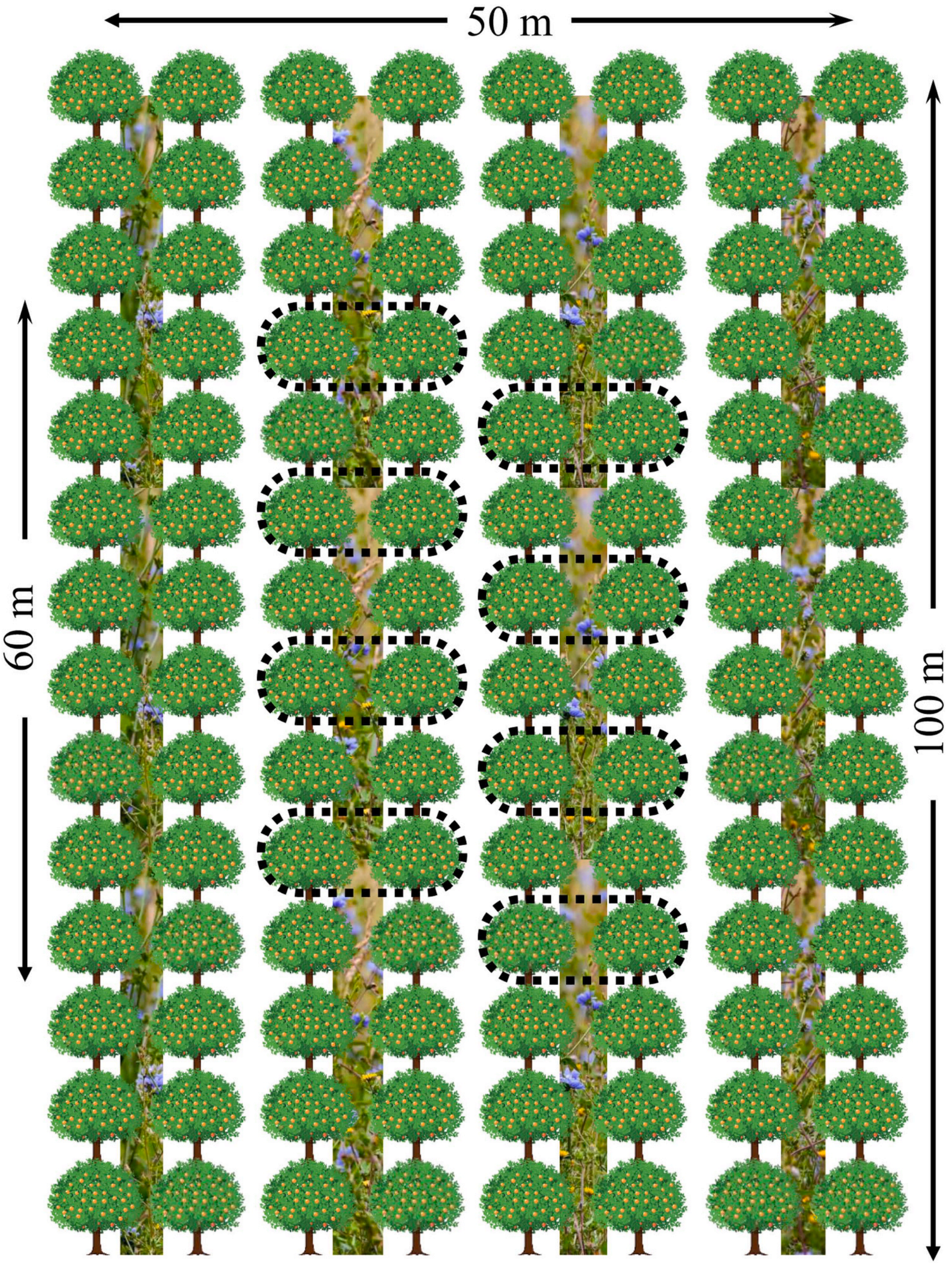

Fig. 1. Schematic diagram of a 0.5 ha experimental plot consisting of eight rows of orange trees and seven alleyways. Wildflower strips were established in alternate alleyways. Black dashed lines show the paired trees sampled throughout the three-year study.

Fig. 2. A baited card, prepared by sticking approximately 450 ± 50 *Ephestia kuehniella* eggs to a 10 mm×10 mm area of graph paper, mounted in the citrus canopy using a staple and left *in situ* for seven days before collected and the predation rate assessed.

Where possible, all Araneae, Coleoptera, Hemiptera, Neuroptera, Hymenoptera, and Diptera (Syrphidae) involved in pest regulation (Bellows and Fisher, 1999) were identified to morpho-species. If morpho-species could not be determined, individuals were identified to the next lowest rank, which enabled the functional group, based on trophic function, to be determined (genus or family). Many ant species predate citrus crop pests but they can also disrupt biological control by attacking natural enemies, consequently they were classed as their own functional group (Pekas *et al.*, 2011). In total, four non-taxonomic functional groups were determined, parasitoids, predators, hyper-parasitoids, and ants (Appendix A3).

2.4. *Pest regulation services*

Pest regulation services in the orange trees were determined immediately subsequent to sampling arthropods from the canopy to ensure predation rates could be directly related to natural enemy abundances. Cards baited with sterile *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs were used to quantify pest regulation services (Campbell et al., 2017). The baited cards consisted of 60 mm × 10 mm strips of graph paper (120 gsm). The upper most 10 mm × 10 mm of the card was covered with Henkel® Pritt roller tape and covered with *E. kuehniella* eggs. Excess eggs were removed with a camel-hair brush so that the remainder covered the paper as a single layer. The total number of eggs was counted from alternate rows of the prepared area (five of the ten columns of the graph paper) and then multiplied to estimate the total number of eggs on the card before predation. Each prepared card held approximately 450 ± 50 *E. kuehniella* eggs. Cards were mounted in the tree canopy (≈ 2 m height) by wrapping the excess graph paper around a randomly selected branch and fastening with a staple (Fig. 2). The baited cards were left *in situ* for seven days, after which the number of eggs remaining was estimated by counting half the area, as previously described. This was repeated with fresh baited cards every 28 days for May, June, and July of year two and from April to October in year three. Six to eight cards were mounted per plot in year two and was increased to 16 per plot in year three.

2.5. *Statistical analyses*

All statistical analyses were performed using RStudio (RStudio Team, 2015) Version 1.3.1056 for R version 4.0.2 (R Core Team, 2019).

2.5.1. *Natural enemy richness*

The influence of alleyway management on natural enemy richness was investigated using a negative binomial distribution generalised linear mixed effects model (GLMM). Where it was not possible to identify an individual to species, it was assumed that the identified rank (genus or family) contained one species. The number of natural enemy species was set as the response variable. The predictor variables were alleyway treatment and study year, which were set as fixed factors. Orchard block and sampling date were included as random factors. Goodness of fit was visually verified by plotting Q-Q plot with standardised residuals and checking dispersion. The model was reduced to the most parsimonious, in which the interaction between treatment and year was removed, and a null model was generated to infer any treatment effect.

2.5.2. *Natural enemy composition*

Species composition of the natural enemies was first visually examined between treatments and sites using non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity metric. Then, a negative binomial multivariate model was constructed using the mvabund package (Wang et al., 2012). The 72-vector matrix of species abundances was regressed against treatment, year and orchard block, including their interactions. The model was reduced to the most parsimonious model in which all interaction terms were dropped. To infer any treatment effect, the final model was then compared against a null model using ANOVA. Multivariate test statistics were obtained via the Likelihood-Ratio-Test and the *P*-value estimated via 999 PIT-trap resamples (Warton et al., 2017).

2.5.3. *Functional composition of natural enemies*

To investigate the influence of alleyway treatment on the relative abundance of the different functional groups recorded (parasitoids, predators, hyper-parasitoids, and ants), a separate binomial generalised linear model (GLM) was fitted for each of the three study years. The response variable in each was a two-vector matrix including the total abundance of each function group and the total abundance of all other specimens from each alleyway. The explanatory variables were treatment and functional group, including their interaction, and orchard block. In all models, the orchard block was found to be non-significant

Table 2
Mean abundance of arthropod functional groups sampled from the citrus canopy between treatments: control; establishing wildflower strips (EWS); active management wildflower treatment (AMWT); and standard management wildflower treatment (SMWT), and across study years: one, two and three. The number in parenthesis is the standard error about the mean (SEM).

Year	Treat	Mean predators	Mean primary parasitoids	Mean hyperparasitoids	Mean unknown parasitoids	***Mean ants***
One	Control	5.42 (± 0.76)	1.44 (± 0.41)	0.54 (± 0.18)	1.81 (± 0.33)	1.83 (± 0.48)
One	EWS	6.08 (± 0.88)	1.31 (± 0.24)	0.50 (± 0.17)	2.73 (± 0.54)	1.96 (± 0.56)
Two	AMWT	8.04 (± 0.77)	4.18 (± 0.95)	1.11 (± 0.31)	5.66 (± 1.0)	3.77 (± 0.78)
Two	Control	7.61 (± 1.46)	3.43 (± 0.80)	0.75 (± 0.16)	3.46 (± 0.69)	8.32 (± 2.97)
Two	SMWT	8.55 (± 1.03)	5.18 (± 0.89)	0.98 (± 0.19)	6.18 (± 0.69)	6.00 (± 1.27)
Three	AMWT	16.23 (±1.53)	6.88 (±1.00)	0.81 (± 0.21)	4.04 (± 0.67)	4.50 (± 1.38)
Three	Control	15.02 (± 1.89)	6.58 (± 0.98)	1.69 (± 0.42)	3.69 (± 0.53)	5.06 (± 1.10)
Three	SMWT	19.88 (± 2.02)	16.92 (± 3.13)	1.81 (± 0.39)	5.27 (± 0.79)	6.35 (± 1.41)
Total	*7233*	*2306*	*416*	*1699*	*1999*	

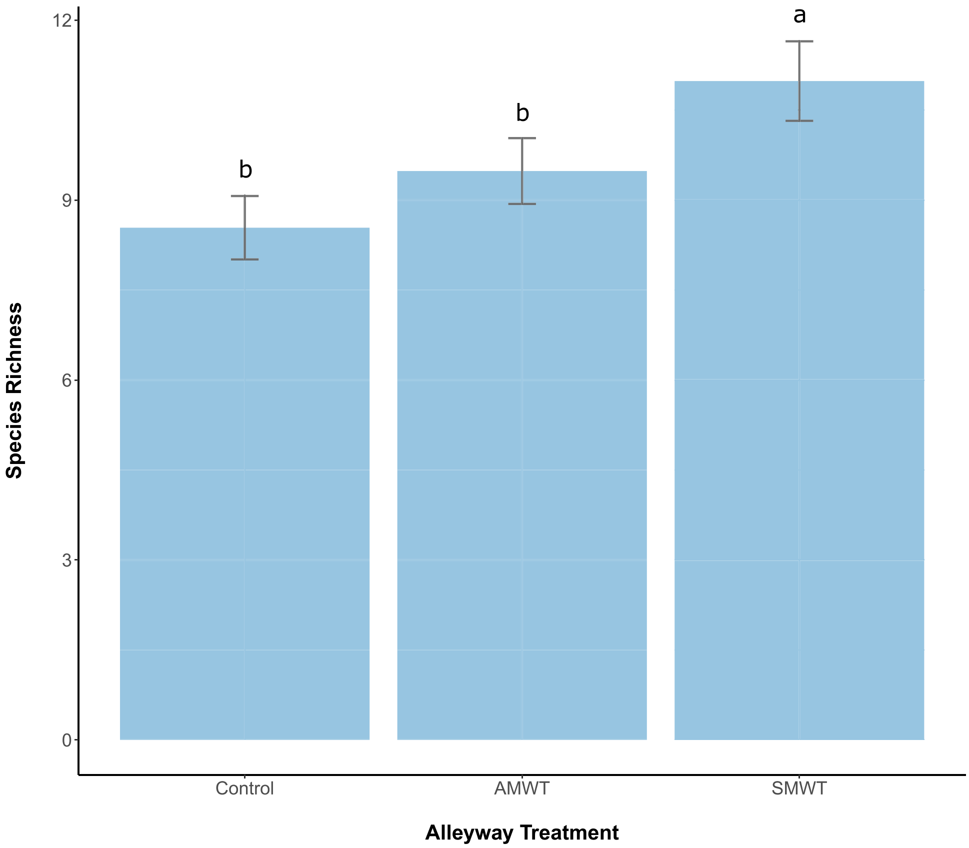

Fig. 3. Mean natural enemy richness in the citrus canopy in response to alleyway management: control, active management wildflower treatment (AMWT) and standard management wildflower treatment (SMWT). Error bars represent ± 1 SEM.

and was dropped. The final model was then compared using ANOVA to null models, in which the treatment × functional group interaction was removed for both models. Goodness of fit was verified by plotting the residuals (y) against the estimated responses (x) to check for dispersion and equal distribution about $y = 0$. Pairwise comparisons were explored via emmeans (Lenth et al., 2022).

2.5.4. *Pest regulation services*

To investigate the influence of alleyway treatment on pest regulation services, a binomial GLM was fitted for years two and three when the baited card experiment was conducted. The response was a two-vector matrix composed of the number of eggs remaining on the card after seven days and the number predated from the cards during the same period. The explanatory fixed factor variables were alleyway treatment and month. Orchard block was included as a random effect. Goodness of fit for each model was determined as previously described. The final model was then compared using ANOVA to a null model, in which treatment as a factor was removed.

3. Results

Over the three-year study, a total of 13,691 arthropods were identified from the tree canopy following vacuum sampling. Of these, 9539 individuals (69.4%) were natural enemy species belonging to 26 families; 2306 (16.8%) of the natural enemies were identified as primary parasitoids, 7233 were predators (52.8%), and 38 (0.3%) were omnivores. A further 416 of the total arthropods recorded were identified as hyperparasitoids (3%) belonging to eight genera, and 1999 ants belonging to four genera. An additional 1699 parasitoids were collected and categorised as ‘unknown parasitoids’ (12.4% of total individuals collected). As they were only identified to family this prevented their categorisation in relation to pest regulation (Table 2).

3.1. *Natural enemy richness in the canopy*

Across the three-year study, the richness of natural enemy species recorded in the citrus canopy was influenced by alleyway treatment (ANOVA: df = 2, $\chi^2 = 12.072$, $P = 0.002$). The richness was approximately 25% higher in the canopy adjacent to SMWT (mean richness = 10.98 species per 0.25 m^2 ± 0.66 SEM) than in the control (mean richness = 8.54 ± 0.53 SEM) (Fig. 3). In contrast, species richness in the canopy adjacent to AMWT (mean richness = 9.48 ± 0.55 SEM) was similar to the control. This effect was consistent across all study years, as the most parsimonious model dropped the interaction between alleyway treatment and study year.

3.2. *Natural enemy composition and functional abundance*

The community composition of natural enemies was not influenced by alleyway treatment (anova.manyglm: df = 6, LR = 446.5, $P = 0.294$) (Fig. 4a). However, separation of communities was observed between orchard blocks in the south of Huelva (La Calvilla and Madre del Agua) and orchard blocks in the north of Huelva (Montepinos 1 and 2) (Fig. 4b).

The relative abundance of the five different functional groups was influenced by alleyway treatment in years two (ANOVA: $\chi^2 = 198.49$, df = 18, $P < 0.001$) and three (ANOVA: $\chi^2 = 188.14$, df = 18, $P < 0.001$). However, the relative abundance of the different functional groups was similar across treatments in the establishment year (ANOVA: $\chi^2 = 7.791$, df = 4, $P = 0.100$) (Fig. 5).

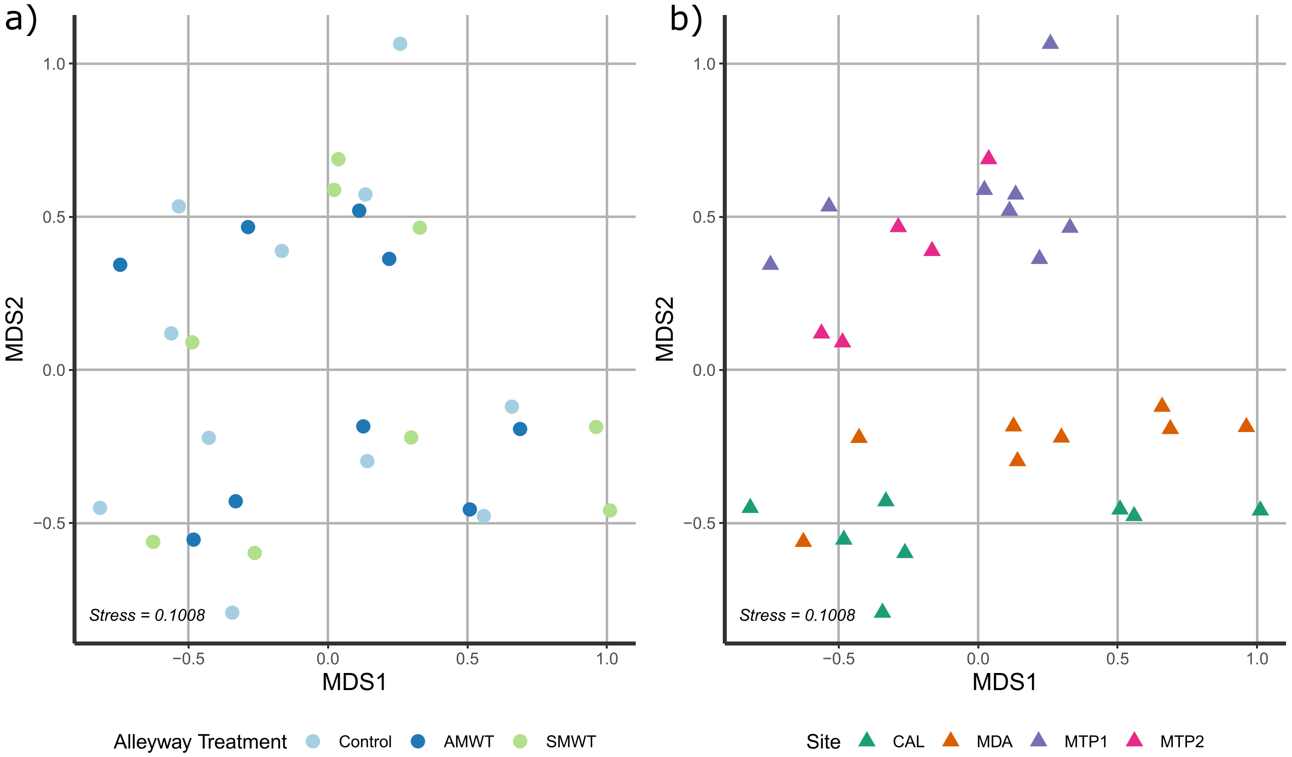

Fig. 4. Biplot of non-metric multidimensional scaling (nMDS) using Bray-Curtis dissimilarity. The points correspond to site indices. Points are coloured to visualise community separation according to treatment a), where the control is pale blue, active management wildflower treatment (AMWT) are dark blue, and standard management wildflower treatment (SMWT) are dark green circles; and according to site a), where La Calvilla (CAL) are teal, Madre del Agua (MDA) are orange, Montepinos 1 (MTP1) are purple, and Montepinos 2 (MTP) are pink triangles.

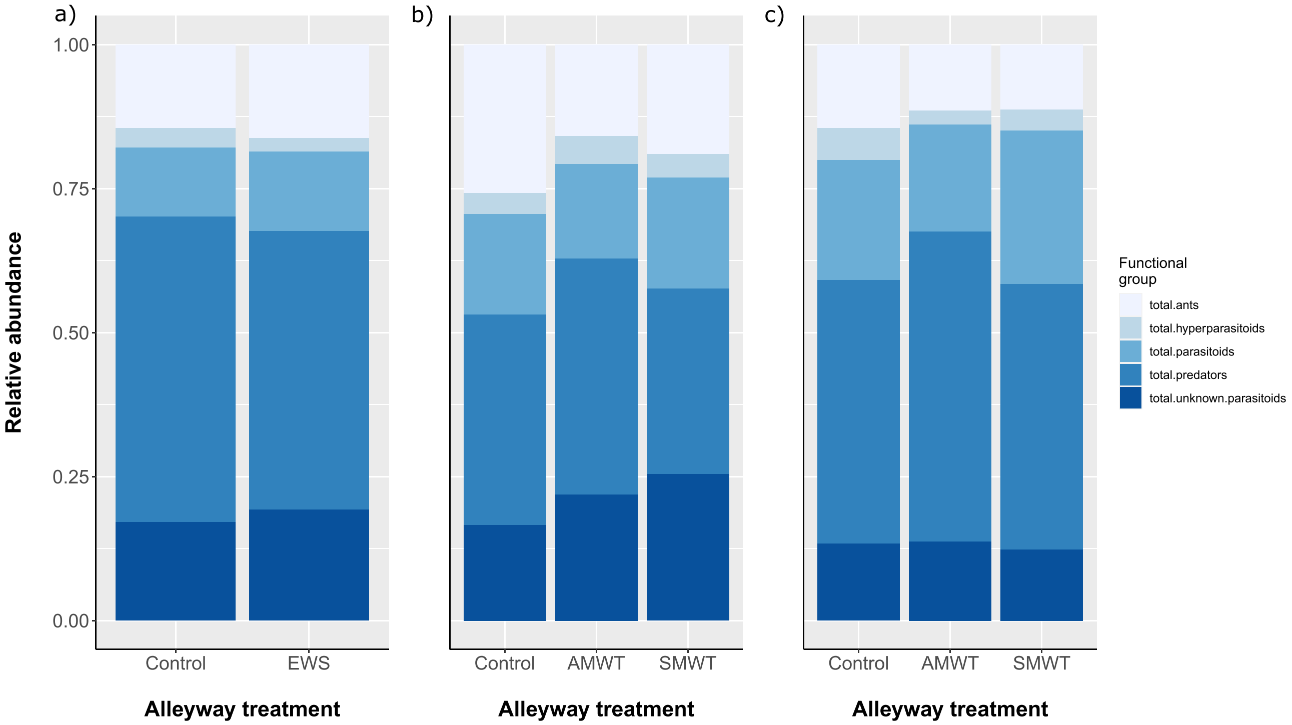

Fig. 5. Relative abundance of natural enemy abundance according to functional group according to the alleyway management treatments; control and establishing wildflower strip (EWS) in year one a), and control, active management wildflower treatment (AMWT), and standard management wildflower treatment (SMWT) in years two b) and three c).

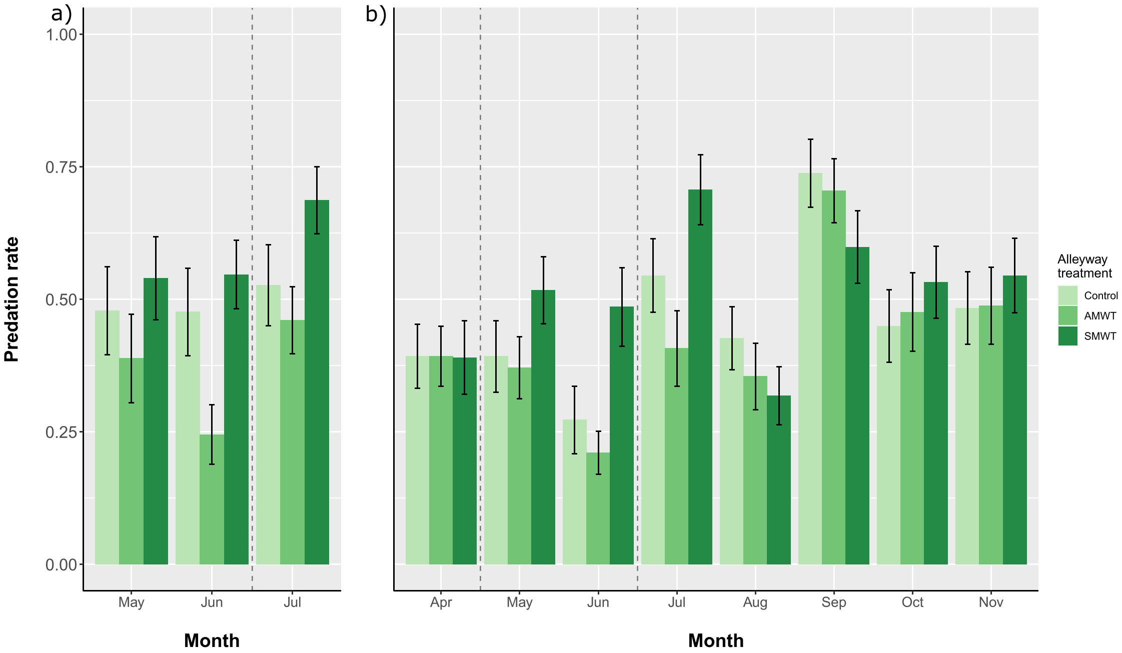

Fig. 6. Predation rates per baited card, represented as the mean proportion of eggs depleted per card in response to the alleyway management treatment: control (light green), active management wildflower treatment (AMWT: medium-green), and standard management wildflower treatment (SMWT: dark green), in years two a) and three (b). The vertical grey dashed lines represent when alleyways were cut in the active management wildflower treatment. Error bars represent ± 1 SEM.

Fig. A.2. Treatment plots; a) Control treatment, managed conventionally by cutting throughout the season to keep the vegetation low; b) Standard management wildflower treatment, cut once annually, allowed to grow tall and complex; c) Active management wildflower treatment, cut three times annually to approximately 10 cm to encourage spill-over of natural enemies onto the crop.

3.3. Pest regulation services

In year two, during May, June and July, alleyway treatment significantly affected predation rates in the canopy (ANOVA: $\chi^2 = 3799.1$, df $= 2$, $P < 0.001$). Although the total predation rates between months varied (ANOVA: $\chi^2 = 1303.6$, df $= 2$, $P = 0.052$), the proportion of eggs predated was consistently greater with SMWT alleyways irrespective of sampling month (ANOVA: $\chi^2 = 640.5$, df $= 4$, $P = 0.575$) (Fig. 6a). Orchard block also significantly affected predation rates (ANOVA: $\chi^2 = 3059.6$, df $= 2$, $P > 0.001$).

In year three, predation rates in the canopies were also affected by alleyway treatment (ANOVA: $\chi^2 = 2002$, df $= 2$, $P = 0.014$) (Fig. 6b). Again, the total predation rates between months varied (ANOVA: $\chi 2 = 16079$, df $= 7$, $P < 0.001$). Although the proportion of eggs predated tended to be greater in SMWT alleyways, this treatment effect was not consistent across all sampling months (ANOVA: $\chi^2 = 5509$, df $= 14$, $P = 0.051$), with the highest predation rates in June and early July. Orchard block also significantly affected predation rates (ANOVA: $\chi^2 = 19940$, df $= 1$, $P < 0.001$).

4. Discussion

This is the first study to demonstrate that wildflower strips, composed of native perennial forb and grass species, can increase the abundance and richness of natural enemies in the adjacent orange tree canopies, leading to enhanced pest regulation services. However, this was not realised until the third year of study, and then, only in association with the standard management wildflower treatment (SMWT). During the establishment year (year one) and the first year that the distinct management strategies were applied to the sown wildflower alleyways (year two) the wildflower treatments did not increase natural enemy abundance in the citrus canopies relative to the control treatment. This finding is similar to that observed by Silva et al. (2010) in lemon and is most likely a consequence of the wildflower strips still developing following sowing (Mateos-Fierro et al., 2021; Westbury et al., 2017; Woodcock et al., 2005) and a delayed response to the new treatments in year two (Denys and Tscharntke, 2002). In year three, however, SMWT showed significantly greater natural enemy richness and abundance in the citrus canopy over other treatments. Furthermore, this was associated with enhanced pest regulation services.

As the positive response of pest regulation associated with SMWT was specific to late spring and early summer, it is important to note that this is a crucial period for several key citrus pest species, such as *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), *Planococcus citri* Risso (Hemiptera: Pseudococcidae), *Panonychus citri* (McGregor) (Acari: Tetranychidae), and *Aleurothrixus floccosus* (Maskell) (Hemiptera, Aleyrodidae) (Urbaneja et al., 2009, 2015, 2020). As such, pest regulation services provided by native and naturalised natural enemies during this period are essential to their successful regulation and successfully mitigating economic losses (Bouvet et al., 2019; Martínez-Ferrer et al., 2003; Vanaclocha et al., 2011). However, when the wildflower strips were managed under active management (AMWT), pest regulation services were comparable to rates observed in the control plots, or lower. Taller uncut vegetation, as in SMWT, supports a greater natural-enemy-to-pest ratio within habitats (Meyer et al., 2019). As such, under increased resource competition, natural enemies spill-over from these habitats and bolster pest regulation services on the crop (Campbell et al., 2017; Rand et al., 2006).

In contrast to SMWT, AMWT applied to force spill-over of natural enemies onto the crop was associated with reduced richness and abundance in the tree canopies and diminished pest regulation services, suggesting the strategy was unsuccessful. In contrast to what was expected, AMWT may not offer enough high-quality resources to augment natural enemy populations (Mockford et al., 2023) to facilitate spill-over (Herz et al., 2019). Natural enemies require plant derived resources, such as sugars (nectar, guttation and honeydew), proteins (pollen and alternative prey/hosts), shelter (from disturbances and extreme temperatures) and refuge (from predation) (Gurr et al., 2017), which were hypothesised to be provided by the novel wildflower strips developed for this study. However, the plant community in AMWT was slow to recover from cutting and by the final year of the study, the sward tended to contain more bare ground, was shorter in height, less structurally complex, and was becoming dominated by grasses (Mockford et al., 2023). Such compositional and structural changes can have a significant impact on the resource availability and accessibility (Mockford et al., 2022; Westbury et al., 2017), intra-guild interactions (Woodcock et al., 2009), and the suitability as refuge (Humbert et al., 2012) and shelter habitats (Dennis et al., 1994). Natural enemies optimise foraging to enhance energy reserves whilst minimising fitness costs incurred through searching, disturbance, and predation/parasitism (Andersson, 1981; Charnov, 1976). It is likely then that they responded by migrating away from the low quality patches of high disturbance and diminished resources associated with AMWT. Furthermore, cutting itself increases direct arthropod mortality from the machinery; up to 88% arthropod mortality dependent on the machinery (Humbert et al., 2009; Mazalová et al., 2015). It is possible that cutting to a greater height, such as 20 cm (Mateos-Fierro et al., 2021) or only partially cutting the sward to maintain a refuge area (Humbert et al., 2012) may have maintained plant derived resources to better supported natural emeies in AMWT.

The difference in species composition of natural enemies between geographical locations could be due to differences in landscape composition and management between northern and southern sites (Woltz et al., 2012). Although all sites were located within anthropogenic mosaic landscapes, southern Huelva is characterised by a greater diversity of crop types, including perennial and annual systems, while northern Huelva includes lower diversity of crop types and instead larger areas of managed Eucalyptus forest, Dehesa, and shrubland (Navarro-Cerrillo et al., 2023). Although the alleyway treatment did not impact species composition, it did alter the relative abundance of different functional groups. Vercher et al. (2012) recorded a significant decline in primary parasitoid abundance after the orchard alleyway habitat was cut, likely due to the reduced resources available to support them (Mockford et al., 2022). Additionally, the relative abundance of hyperparasitoids in the canopy with SMWT and AMWT in year three was half that of the control. Hyperparasitoids are known to disrupt the regulation of aphids by their primary parasitoids in citrus orchard systems, especially later into the year (Gómez-Marco et al., 2015). Hence, a reduction in their relative abundance with AMWT and SMWT might translate to enhanced pest regulation services. The control treatment was also characterised by lower abundance of parasitoids of unknown function, suggesting a reduction in the wider biodiversity which is typically supported by wildflower plantings (Šálek et al., 2022; Schmidt et al., 2022).

AMWT supported no greater species richness than the control. This suggests alleyway resources were limiting and unable to support natural enemies, and hence unable to facilitate spill-over of natural enemies into the crop canopy. Although AMWT promoted the sown tussock-forming grass species within the sown alleyways (Mockford et al., 2023), which are typically associated with a more stable microclimate and can shelter insects from adverse climatic conditions (Collins et al., 2003; Luff, 1965; MacLeod et al., 2004), cutting to a height of 10 cm in both May and July is likely to have strongly affected the structure and function of the alleyway habitat, and removed shelter during the hottest and driest part of the year, preventing the habitat from recovering (Morris, 2000). Cutting also reduced the cover abundance of some of the sown forb species, such as *Psoralea bituminosa*, *Salvia verbenaca, Hypericum perforatum,* and *Cichorium intybus* (Mockford et al., 2023), which without cutting are expected to help support natural enemies by increasing the abundance and diversity of open flowers throughout the year (Mateos-Fierro et al., 2021). *Salvia verbenaca*, for example, provides flowers in early spring and autumn (Blamey and Grey-Wilson, 2004). It is likely that the removal of above-ground biomass for two consecutive years impacted the ability of the plant community to recover (Morris, 2000) and led to the reduced abundance and richness of natural enemies observed in year three. In the standard management treatment, however, sown forb species were retained in the wildflower strip, and tussock-forming grasses were able to grow taller through less frequent cutting, which boosted plant richness and the provision of resource for natural enemies.

5. Conclusions

This study has demonstrated that natural enemy richness and relative abundance of beneficial arthropods in the citrus canopy can be enhanced by sowing perennial wildflower strips in alleyways, but only when they are allowed to grow throughout the season, as with SMWT. Furthermore, such wildflower strips, designed to provide important resources in the alleyways, can bolster pest regulation services in the adjacent canopy. This study has also highlighted the importance of ongoing management strategies applied to wildflower strips, especially under Mediterranean climates as this can influence not only the plant communities but also natural enemy community structure, and ultimately the delivery of pest regulation services. Further studies are required to determine how such ecological intensification strategies influence pest-natural enemy dynamics in the field.

CRediT authorship contribution statement

Alice Mockford: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alberto Urbaneja:** Writing – review & editing, Supervision, Methodology. **Kate Ahsbrook:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Duncan B Westbury:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data will be made openly available

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Appendix A.1. Detailed site description

The study was conducted in four sweet orange (*Citrus sinensis* Osbeck cv. Navel) orchards within three farms (sites), Madre del Agua, La Calvilla and Montepinos, at two different localities in the province of Huelva, south-west Andalusia, Spain (Appendix 3.2). Huelva is an important citrus growing region of Spain; characterised by a sub-tropical Mediterranean climate, with an average annual temperature of 17°C, and annual precipitation of 525 mm (AEMET, 2020). The farm of Montepinos was situated in the north of Huelva (37°47’43.21 N 6°56’21.11 W) at 351 m elevation and characterised by clay soil. The farms Madre del Agua (37°26’27.80"N 7° 9′55.73"W) and La Calvilla (37°24’10.95"N 7° 3′42.67"W), were situated in the south of Huelva at 159 m (Madre del Agua) and 153 m (La Calvilla) of elevation and both characterised by sandy soil. The two localities were 42.59 km apart.

Orchards were selected to meet the following selection criteria:

1. Citrus producers Martinavarro S.L. (Almassora, Spain) and Vicente Giner S.A. (Beniflá, Spain) offered orchards to be used for the study.
2. Orchards were planted with Navel oranges, consisting of varieties with similar phenology and management strategies. Plant phenology significantly affects the pest status of phytophagous arthropods (Williams and Dixon, 2007). Citrus varieties with different phenology may experience pest outbreaks at different times of the year (Franco *et al.*, 2004). As such, all treatment plots were established in late cropping Navel cultivar, Lane Late, Rohde and Powel, which all have similar phenology and management requirements (IVIA, 2016).
3. Orchards were at least eight years old and no older than 50 years. Citrus trees take eight years to reach full productivity (Ferguson and Grafton-Cardwell, 2014) and peak productivity typically extends no further than 50 years of age (Ferguson and Grafton-Cardwell, 2014; Wang *et al.*, 2015). The maturity of the citrus trees also influences their susceptibility to attack from different pest species (Llorens Climent and Martín Gil, 2014). Madre de Agua was the most mature orchard, established in 1994, La Calvilla was established in 2008, and Montepinos in 2007.
4. Orchards did not contain any other sown habitat or have natural habitat within 150 m of the treatment plots. The presence of alternative non-cropped habitat within foraging distance of the treatment plots may increase spill-over of natural enemy into the experimental plots or dispersal out of the experimental plots (Lindgren, Lindborg and Cousins, 2018). Even small fragments of non-cropped habitat can sustain natural enemies and act as islands, which facilitate dispersal between experimental plots and would reduce independence within the study design (Knapp and Řezáč, 2015).
5. Orchards were of sufficient area to accommodate the randomised block design. To reduce interference between plots, the three experimental treatment plots, each 100 m x 50 m (0.5 ha) and spaced at least 150 m from one another, must be situated within the same orchard. Each plot must be no closer than 7.5 m from the orchard boundary or any other anomalies in the topography such as trenches and gullies.

As a result of these criteria, four orchards were identified in Huelva, Andalusia; Madre del Agua, La Calvilla, Manzorrales, and Montepinos, and select for use in the study. Due to poor drainage in Manzorrales, which resulted in poor establishment of the wildflower habitat, this site was discontinued after the establishment year (2017). Madre de Agua was the most mature orchard, established in 1994, La Calvilla was established in 2008, and Montepinos in 2007. Madre de Agua contained Lane Late, La Calvilla contained Powell, and Montepinos contained Rohde and Powell.

Appendix A.2. Orchard management

The study was conducted within commercial *Citrus* orchards managed under IPM guidelines (Llorens Climet and Martín Gil, 2014). All treatment plots within a single block were managed the same, which included applications of chemical pesticides when deemed necessary by the growers (Table 1). Calendar applications of pesticides were used for the control of California red scale, *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), across all farms. In Montepinos 15% spirotetramat, a systemic acetyl-CoA carboxylase inhibitor, was applied once annually to coincide with the first generation of *A. aurantii*. In Madre del Agua and La Calvilla, two annual pesticide treatments to control *A. aurantii* were applied to coincide with the first two generations. In these orchards (Madre del Agua and La Calvilla), spirotetramat, organophosphates (chlorpyrifos) and juvenile hormone mimics (pyriproxyfen) were applied in rotation. In Montepinos, annual applications of flonicamid, a chordotonal organ inhibitor, were applied in spring to control aphids, organophosphates in mid-summer for the control of coccids (Coccidoidea), and abamectin, a chlorine channel activator, in late summer to control citrus leaf miner (*Phyllocnistis citrella* Stainton; Lepidoptera: Gracillariidae). Across all orchard sites, another acetyl-CoA carboxylase inhibitor, spirodiclofen, was applied at the end of summer, at least once annually for the control of *Eutetranychus* mites (Acari: Tetranychidae). The orchard Madre del Agua was treated at least once annually with spinosyns, a nicotinic acetylcholine receptor allosteric modulator, when populations of Mediterranean fruit fly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae), reached the action threshold. Likewise, population of *C. capitata* at La Calvilla were treated when they approached the action threshold, typically with the pyrethroid pesticide, lambda-cyhalothrin.

Fig. A.1. Location of the three orchards in relation to a) the Iberian Peninsula and b) the province of Huelva, south west Spain.

Table A.2
Chemical intervention for the control of citrus pests in the study orchards: the target organisms, products used, typical timing of application, and the type of monitoring used to determine intervention.

Target organism	Product	Month	Criteria for intervention (life cycle dependent / field captures / crop sampling)
Aonidiella aurantii	Spirotetramat, Chlorpyrifos, or Pyriproxyfen	May/June and July/August	Life cycle dependent
Aphidoidea	Flonicamid	May	Crop sampling
Tetranychidae	Spirodiclofen	August to October	Crop sampling
Phyllocnistis citrella	Abamectin	August	Crop sampling
Coccidae	Chlorpyrifos	August	Crop sampling
Ceratitis capitata	Spinosyns or Lambda-cyhalothrin	October	Field captures

All orchards were irrigated via underground systems, and fertilisers applied directly into these irrigation systems (fertigation). Conventional management practices of the orchard alleyways included regular cutting of the naturally occurring vegetation to less than 5 cm in height, four to five times annually. During the winter months, the naturally occurring vegetation of the alleyways was allowed to grow until the first cut of the year. Debris pruned from the citrus trees, typically in late spring, was discarded in the alleyways and a tractor mounted disc mulcher used to shred it.

Shredded plant material was then left *in situ*.

Appendix A.3. Functional abundance

Table A.3
Orders and families that included in the four different functional groups.

Functional group	Order	Family
Predator	Araneae	Salticidae
Predator	Araneae	Araneidae
Predator	Araneae	Clubionidae
Predator	Araneae	Cheiracanthiidae
Predator	Araneae	Sparassidae
Predator	Araneae	Lycosidae
Predator	Araneae	Oxyopidae
Predator	Araneae	Thomisidae
Predator	Araneae	Other Araneae
Predator	Coleoptera	Coccinellidae
Predator	Coleoptera	Carabidae
Predator	Coleoptera	Staphylinidae
Predator	Hemiptera	Nabidae
Predator	Hemiptera	Reduviidae
Predator	Hemiptera	Anthocoridae
Predator	Neuroptera	Chrysopidae
Predator	Neuroptera	Hemerobiidae
Predator	Neuroptera	Myrmeleontidae
Predator	Neuroptera	Coniopterygidae
Predator	Diptera	Syrphidae
Primary parasitoids	Hymenoptera	Aphelinidae
Primary parasitoids	Hymenoptera	Braconidae
Primary parasitoids	Hymenoptera	Encyrtidae
Primary parasitoids	Hymenoptera	Eulophidae
Primary parasitoids	Hymenoptera	Pteromalidae
Primary parasitoids	Hymenoptera	Scelionidae
Primary parasitoids	Hymenoptera	Chalcididae
Ants	Hymenoptera	Formicidae
Hyperparasitoids	Hymenoptera	Aphelinidae
Hyperparasitoids	Hymenoptera	Encyrtidae
Hyperparasitoids	Hymenoptera	Pteromalidae
Hyperparasitoids	Hymenoptera	Figitidae
Hyperparasitoids	Hymenoptera	Cynipidae
Hyperparasitoids	Hymenoptera	Megaspilidae
Other parasitoids	Hymenoptera	Aphelinidae
Other parasitoids	Hymenoptera	Braconidae
Other parasitoids	Hymenoptera	Encyrtidae
Other parasitoids	Hymenoptera	Trichogrammatidae
Other parasitoids	Hymenoptera	Eulophidae
Other parasitoids	Hymenoptera	Pteromalidae
Other parasitoids	Hymenoptera	Scelionidae
Other parasitoids	Hymenoptera	Figitidae
Other parasitoids	Hymenoptera	Ceraphronidae
Other parasitoids	Hymenoptera	Diapriidae
Other parasitoids	Hymenoptera	Eurytomidae
Other parasitoids	Hymenoptera	Ichneumonidae
Other parasitoids	Hymenoptera	Tetracampidae

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