



Structural heterogeneity of wildflower strips enhances fructose feeding in parasitoids

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ABSTRACT

The use of wildflower strips to provide carbohydrate resource for parasitoids and enhance pest regulation is widely recommended in agriculture. However, how the management of wildflower strips affects resource availability and utilisation by parasitoids has never been studied. Using orange orchards as a model system, three experimental alleyway management treatments were investigated: a control treatment where naturally occurring vegetation in the alleyways between rows of trees was managed under standard farm practice; a standard management wildflower treatment in which sown wildflower strips in alleyways were managed by cutting once a year; and an active management wildflower treatment, in which the wildflower strips in alleyways was managed by cutting three times a year. Wildflower strips under standard management prevented the seasonal decline of nectar, supporting fructose feeding in parasitoids across all three seasons. The abundance of floral and hemipteran honeydew carbohydrate resources in the orchard alleyways and citrus canopy was consistently greater with the standard management treatment than the control or the active management treatments. In turn, this treatment was associated with twice the abundance of primary parasitoids than with the control and active management treatments in both summer and autumn. In addition, in autumn, parasitoids were more likely to have recently fed on carbohydrate in the standard management treatment than in the other two alleyway treatments. Finally, greater carbohydrate feeding in parasitoids was associated with increased structural heterogeneity of vegetation within the orchard alleyways. This study demonstrates that the nutritional status of parasitoids in a perennial cropping system can be improved using wildflower strips, which could enhance pest regulation, and emphasises the importance of studying the management of wildflower strips when targeting specific resource requirements.

1. Introduction

Natural enemies of crop pests provide a valuable pest regulation service to agriculture (Jervis, 2005). Parasitoids are a key group of natural enemies as they are responsible for successfully regulating a diverse range of agricultural pest species (Jervis, 2005). Consequently, there is a strong rationale for supporting parasitoids in food crop systems to maximise their pest regulation potential (Gurr et al., 2017). This can be achieved through the provision of suitable carbohydrate resources, including nectar and honeydew, which increases both the longevity and fecundity of parasitoids (Tena et al., 2016; Benelli et al., 2017). However, in intensively managed agricultural landscapes, the availability of

carbohydrate resources is often limited both spatially and temporally (Heimpel, 2019). In these landscapes, carbohydrate resources are typically limited to brief flowering periods of nectar-producing plants (predominantly crops) and when honeydew-producing hemipteran pests or plant leachates are present (Lundgren, 2009; Tena et al., 2016; Urbaneja-Bernat et al., 2020). As such, parasitoids are more likely to be carbohydrate deficient in cropped habitats compared to semi-natural areas which are typically associated with a higher diversity of flowering plants (Kishinevsky et al., 2017). This imbalance led to the development of the ‘parasitoid nectar provision hypothesis’, which states that the creation of alternative wildflower habitats within fields can decrease pest pressure through the provision of nectar (Heimpel and Jervis,

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2005).

The parasitoid nectar provision hypothesis is now a cornerstone of habitat management for pest regulation (Gurr et al., 2017). In orchard systems perennial wildflower strips are typically established in alleyways between rows of fruit trees; this strategy can successfully manage pest populations in a variety of fruit crops, including apple (Albrecht et al., 2020) and cherry (Mateos-Fierro et al., 2021). However, the impact of wildflower strips on parasitism rates in the crop can be highly variable and the fundamentals of this hypothesis have been called into question (Heimpel, 2019). Nonetheless, there is evidence from orchard systems that nectar-producing plants from adjacent semi-natural habitats can enhance the incidence of parasitoids which have recently fed on fructose (Kishinevsky et al., 2017), a common monosaccharide carbohydrate in nectar and honeydew which parasitoids cannot synthesise themselves (Heimpel et al., 2004). In citrus orchards, parasitoids feed on hemipteran honeydew when wildflowers are scarce (Tena et al., 2013b) and supplementary sugar can enhance parasitoid fecundity, increasing population density, and ultimately enhancing pest regulation services (Tena et al., 2015). However, due to differences between sites in plant resources and honeydew-producing Hemiptera species, this can lead to very site-specific responses. By establishing wildflower strips of known seed mix in the orchard alleyways, responses are more likely to be standardised between sites enabling the influence of alleyway management to be investigated.

To maintain the desired plant communities, perennial wildflower strips require regular management by cutting (Westbury et al., 2008). However, the impact of cutting on the provision of resource for parasitoids has not previously been considered. Cutting can affect the structural heterogeneity of the strips and, consequently, arthropod community structure (Woodcock et al., 2009; Blake et al., 2013). In addition, cutting might also be used to encourage the spill-over of natural enemies onto adjacent crops at critical periods of pest incidence (Goller et al., 1997). Conversely, cutting might remove vital resources used by foraging parasitoids. Therefore, to develop an effective approach to boost the abundance of parasitoids and their pest regulation services, there is a need to understand how wildflower management strategies can influence the availability of carbohydrate resources for parasitoids.

Despite the potential benefits of providing increased carbohydrate resources in the farmed landscape, a potential ecosystem disservice of wildflower strips could be an increased fitness of phytophagous crop pests that require nectar for increased longevity and fecundity (Heimpel and Jervis, 2005; Wäckers et al., 2007). Similarly, arthropods of the fourth trophic level, such as hyperparasitoids and parasitoids of predators, might also benefit from the provision of nectar (Araj et al., 2009; Tougeron and Tena, 2019). Under these circumstances, any benefits gained by enhancing fitness of the primary parasitoids of crop pests may be counteracted. Therefore, understanding how the management of wildflower strips affects different insect functional groups is necessary when aiming to maximise the delivery of pest regulation services by parasitoids.

The main aim of this study was to determine the impact of a novel perennial wildflower strip, designed to support natural enemies and managed by cutting to promote spill-over, on the availability of carbohydrate resources and their use by parasitoids. The objectives were: i) to determine the abundance of accessible carbohydrate resource units according to alleyway treatments, ii) to determine the effect of alleyway treatment on carbohydrate feeding in parasitoids, iii) to investigate how alleyway treatment may alter the abundance of different functional groups, and iv) to determine which parasitoid and orchard characteristics best predict carbohydrate feeding.

2. Materials and methods

2.1. Site description and experimental design

The study was conducted during 2019 in three commercial sweet orange (*Citrus sinensis* Osbeck cv. Navel) orchards in the province of Huelva, south-west Andalusia, Spain. Spanish citrus orchards are typically maintained with bare soil, with vegetation either mechanically or chemically removed under the trees and in alleyways; sources of nectar for parasitoids are therefore scarce (Tena et al., 2015; Monzó et al., 2020). However, due to the increased drive for more sustainable approaches to citrus production, producers are now being incentivised to maintain the alleyways between rows of trees with the naturally occurring vegetation which is cut four or five times per year to a height of approximately 5 cm (Arenas-Arenas et al., 2015). Compared to bare soil, this approach can increase the abundance and diversity of natural enemies present in the citrus orchard canopy (Silva et al., 2010). Details of the orange orchards studied are presented in [Supplementary Materials](#) (Appendix A). The experiment was a replicated block design, with one block per orchard (site). Each orchard block contained three 0.5 ha plots, to which three different alleyway treatments were randomly allocated i) a control treatment in which the naturally occurring vegetation of the alleyways was managed conventionally by cutting to ≤ 5 cm four or five times throughout the year, ii) wildflower strips sown in alternate alleyways between rows of orange trees, managed by cutting once annually in February (hereafter standard management), and iii) wildflower strips sown with the same seed mix as used for the standard management wildflower treatment, managed actively by cutting three times per year (≈ 10 cm) (hereafter active management). The active management treatment was timed to coincide with forecasted peak population of a key pest, California red scale, *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), and aimed to increase the movement of natural enemies into the crop. Plots were separated by at least 150 m to help ensure independence between treatments (Brown and Lightner, 1997). To reduce edge effects, the outermost three rows of orange trees from each plot were excluded from sampling and a 20 m buffer zone at either end of each row was established. As such, all carbohydrate resource surveys were conducted and insect samples collected from the inner most four rows of fruit trees, and two alleyways, along a length of 60 m for all treatments (hereafter, sampling area) (Fig. A.3).

The seed mix contained two tussock-forming grass species and 12 forb species that flowered across the year (Table 1; Fig. A.2). The sown wildflower strips were sown in November 2016. Once established, orchards were sampled in three seasons: spring (May), summer (July), and autumn (October) of 2019. For each season, all sites were sampled and surveyed within the same week and all treatment plots at each site were sampled in a single day. The order in which treatment plots were surveyed was randomised.

2.2. Carbohydrate resource availability and accessibility within orchard alleyways and orange tree canopies

To determine the available carbohydrate resource in alleyways, twenty 0.5×0.5 m quadrats were randomly placed and surveyed (10 quadrats per alleyway). In each quadrat, all the floral units of each plant species were identified and recorded, *sensu* Baldock et al. (2015), as well as the number of colonies (units) of honeydew-producing hemipterans. Carbohydrate resource units were the sum of the total number of floral units and the total number of colonies of honeydew-producing Hemiptera recorded per quadrat. Plant leachates were not observed in any plant species and were therefore not included.

Canopy carbohydrate resources were determined from 16 trees within each plot selected from the sampling area. Trees were paired across the alleyway (Fig. A.1.3). In each tree, a 56 cm diameter plastic ring was randomly placed on the canopy adjacent to the alleyway and all the colonies (units) of honeydew-producing species within the ring were

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 ¹Yarrow, ²Bugloss, ³Chicory, ⁴Common shrubby everlasting, ⁵St John's wort, ⁶White hore-hound, ⁷Apple mint, ⁸Yellow restharrow, ⁹Ribwort plantain, ¹⁰Arabian pea, ¹²Wild clary, ¹²Tansy, ¹³Orchard grass, and ¹⁴Tall fescue.

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

identified and recorded (Tena et al., 2015).

Nectar accessibility was determined for all the flower species identified during the carbohydrate resource surveys. Twenty individual flowers of each species were transported to the lab in humid tissue paper sealed in freezer bags. Flowers were dissected longitudinally and the corolla width at the narrowest point was measured under stereomicroscopy using a calibrated ocular graticule. Flowers with trap openings, such as *Psoralea bituminosa* L., were not measured as they are not accessible to parasitoids (Vattala et al., 2006). Flowers with exposed nectaries and plants with extra floral nectaries were assigned an arbitrary corolla width of 3 mm. This width was selected as it was greater than the widest parasitoid head measurement and it was assumed that all parasitoids would have access.

2.3. Vegetation structural heterogeneity

The structural heterogeneity of the alleyway vegetation was determined by calculating the coefficient of variation for each alleyway sampling area. For this, a wooden disc of a standard diameter (30 cm) and weight (200 g) was dropped down a 1 m rule and the height it rested on the sward was recorded (Stewart et al., 2001). Twenty drop disc measurements were taken from each alleyway during each season. The coefficient of variation for each alleyway was expressed as a percentage and calculated using the following formula:

$$CV = \frac{\mu}{\sigma} \times 100$$

Where μ is the standard deviation in drop disc measurements per alleyway and σ is the mean.

2.4. Sampling for parasitoids and *Phyllocnistis citrella* in the tree canopy

Parasitoids and adults of the citrus leaf miner, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), which are highly mobile and require carbohydrates (such as nectar) to complete their life cycle (Parra and Coelho, 2022), were sampled from orange tree canopies using a vacuum sampler adapted from a commercial leaf-blower (Stihl BG 86 C-E), modified as described by Tena, Soto and Garcia-Marí (2008). The same 16 paired trees described above were sampled for each season. In summer and autumn, 16 additional paired trees from the same rows were also sampled. As such, 32 paired trees were sampled per plot during summer and autumn. This increase in sampling effort was to account for an expected lower abundance of parasitoids compared to spring.

The tree canopy adjacent to the alleyway was randomly sampled up to a height of 2 m with four suction of the adapted leaf blower, each for a duration of ten seconds. Each sample consisted of the combined suction from a set of paired trees, eight suction in total. All samples were immediately frozen at -196°C in liquid nitrogen to stop enzyme activity, halting digestion and preserving any carbohydrates in the gut (Tennessee et al., 2014; van Handel, 1985). The samples were then stored on dry ice and transported to the lab where they were stored at -80°C .

2.5. Parasitoid identification, head width measurements, and fructose presence

Insect identification and measurement were conducted on ice. After processing, each specimen was isolated in an Eppendorf®, labelled and returned to -80°C . Parasitoids were identified to species or genus. Parasitoid trophic function (primary parasitoid of a phytophage, hyperparasitoid, or primary parasitoid of an arthropod predator) was

determined, and the primary host assigned (Table A2). Where it was not possible to identify to genus, the parasitoid was identified to family. For these specimens, neither trophic function nor primary host were identified, and they were classified as ‘other’ parasitoids. The head width (taken as the distance from eye to eye) of each individual was measured using a calibrated ocular graticule.

To determine whether parasitoids had recently fed on fructose they were tested with Anthrone reagent (Heimpel et al., 2004). For this, each specimen was first cleaned by vortexing in an Eppendorf® with ~60 °C deionized water. Each washed specimen was placed on a separate microscope slide with 5 µl of the Anthrone reagent and crushed whole under a cover slip to release the gut contents. When fructose consumed by an insect is present, a green-blue colour develops around the crushed insect (Lee and Heimpel, 2003; Segoli and Rosenheim, 2013; Kishinevsky et al., 2017). The colour was allowed to develop for up-to one hour at room temperature (approx. 21 °C), during which it was important to remain vigilant, as in some specimens the green-blue colour developed and then faded. All specimens were then classified as either recently fructose fed or not recently fructose fed.

2.6. Parasitoid and orchard characteristics

The parasitoid phenotypic and functional characteristics were defined as head width, functional group, and honeydew production in the primary host. Orchard characteristics were defined as the number of floral units in the alleyways, number of honeydew producer colonies in the canopy, mean corolla width of flowers per alleyway, and alleyway vegetation structural heterogeneity. In the case of carbohydrate resource units from the alleyway and the canopy, mean counts per 25 cm² quadrat were calculated for each alleyway to provide a representative value for each alleyway.

2.7. Data analysis

All statistical analysis was performed using RStudio (RStudio Team, 2015) R version 1.3.1056 for R version 4.0.2 (R Core Team, 2019). Data manipulation was carried out using the tidyr and dplyr packages (Wickham, 2020; Wickham et al., 2020).

2.7.1. The influence of alleyway treatment on the abundance of carbohydrate resources

To determine if alleyway treatment influences the total abundance of carbohydrate resource available in alleyways or the orange tree canopies, values of carbohydrate resource units (number of floral units and/or honeydew producer colonies) according to treatment were analysed using negative binomial generalised linear models (GLMM) (Bates et al., 2015) for each of the three seasons sampled, spring, summer, and autumn. Values of carbohydrate resource units were regressed against alleyway treatment (control, standard management wildflower treatment, and active management wildflower treatment). A negative binomial error structure was selected to account for zero-inflated count data. To account for the replicate block design, orchard block was included as a random factor. Goodness of fit was verified by plotting the residuals (y) against the estimated responses (x), observing equal distribution about $y = 0$, and by plotting a quantile-quantile (QQ) plot to check for dispersion. ANOVA tables were generated by type II Wald chi-square tests using the CAR package (Fox and Weisberg, 2019). The Multcomp package (v1.4–13) was then used to perform Tukey’s pairwise comparisons between alleyway treatments within each model (Hothorn et al., 2008).

2.7.2. The influence of alleyway treatment on fructose feeding in parasitoids

For each of the three sampling seasons, the proportion of parasitoids that recently fed on fructose was modelled against alleyway treatment using binomial GLMM. The same random effect structure was applied as

described in section 2.6.1. Goodness of fit of the binomial models were verified by comparing the null deviance and residual deviances. ANOVA tables were generated and Tukey’s pairwise comparisons investigated.

2.7.3. The influence of alleyway treatment on the abundance of insect functional groups

Differences in abundance of the five trophic functional groups (three parasitoid functional traits, one phytophage pest and one group for parasitoids ranked to family) for each season were explored using the manyglm function in the mvabund package (v3.9.2) (Wang et al., 2019). To account for the replicated block design, permutations for resampling were restricted to within orchard block using Permute (Simpson, 2019). Negative binomial multivariate generalised linear models were fitted to account for zero-inflated count data, and Monte-Carlo bootstrapping resampled 999 times was used to estimate P -values (Warton et al., 2017). Univariate GLMs fitted to each response vector were then explored to infer the effect of alleyway treatment on each functional trait. Pairwise contrasts between treatments were investigated using multcomp.

2.7.4. Predicting fructose feeding in parasitoids based on parasitoid and orchard characteristics

To explore which factors were most significant in determining parasitoid fructose feeding in the field, fructose feeding was modelled against orchard characteristics and parasitoid phenotypic traits and functional group using generalised linear mixed effects models using lme4 (V1.1–21) in RStudio (Bates et al., 2015). The maximal model was generated using knowledge of parasitoid biology and behaviour and expected ecological interactions. The response variable was a single binary vector composed of each insect’s response to the Anthrone reagent. Treatment was nested within orchard block as random factors and random intercepts also defined for each sample season. Parasitoid and orchard characteristics were considered fixed effects. Two-way interactions were included between the mean carbohydrate resource units in alleyways and the mean carbohydrate resource units in the orange tree canopies, mean carbohydrate resource units in alleyway and alleyway vegetation structural heterogeneity, mean carbohydrate resource units in canopy and alleyway vegetation structural heterogeneity, mean carbohydrate resources units in alleyway and parasitoid head width, and mean corolla width and parasitoid head width. Once the model was fitted, the modes of the random effects were then extracted and the variance plotted to ensure their inclusion within the model was justified (Bates et al., 2015). Initially a subset of the data was used, which included only parasitoids ranked to genus or species ($n = 661$), which permitted trophic function and honeydew production in primary host to be included in the model (Appendix B3). However, as trophic function and honeydew production in primary hosts were found to be non-significant within the model (Table B5), a new model was defined using the whole dataset ($n = 763$).

Automated model selection was then carried out with the ‘Dredge’ function of the MuMIn package (v1.43.17) (Barton, 2020), in which repeated evaluations of all possible subsets of the maximal model were conducted. Models were selected on the basis of second-order Akaike information criterion (AICc) corrected for small sample size, Δ AICc, and model weights. Models with the lowest AICc were considered to be most parsimonious, explaining the largest proportion of variation in the response variable; models where Δ AICc was < 2 are considered to be reasonable (Burnham and Anderson, 2002).

3. Results

3.1. Accessibility of floral nectar to parasitoids

In spring, irrespective of alleyway treatment, 50% of the 231 parasitoids recorded from the orange tree canopies had a head width measuring 0.388 mm or less, 75% measuring 0.464 mm or less, and 95%

measuring 0.599 mm or less (Fig. 1a, spring), with a range of 0.204–1.080 mm. Comparing these measurements with values of mean corolla width (Fig. 1b), nectar was accessible to 100% of parasitoids in all three alleyway treatments. With the standard wildflower management, four different plant species provided accessible nectar to at least 95% of parasitoids, the two sown species *Malva sylvestris* L. (Malvaceae) and *Salvia verbenaca* L. (Lamiaceae) and two unsown species *Daucus* sp. L. (Apiaceae) and *Capsella bursa-pastoris* (L.) Medicus (Brassicaceae). The control and active management also provided accessible nectar to 95% of parasitoids, but only from one plant species: the unsown species *Malva parviflora* in the control alleyways and the sown species *S. verbenaca* in the active management (Fig. 1, spring).

In summer, irrespective of treatment, 50% of the 298 parasitoids recorded in summer had a head width measuring 0.349 mm or less, 75% measured 0.493 mm or less, and 95% measured 0.678 mm or less (Fig. 1a, summer), with a range of 0.154–1.938 mm. Nectar was accessible to at least 95% of parasitoids in all three alleyway treatments. With the standard management and control treatments this was from two different plant species each. In alleyways receiving the standard wildflower management, this was provided by the sown species *S. verbenaca* and the unsown species *M. sylvestris*. In the control, this was provided by the unsown species *Euphorbia chamaesyce* and *Polygonum aviculare*. *Polygonum aviculare* was also present with active management and was the only nectar source available to at least 95% of the parasitoid species (Fig. 1b, summer).

In autumn, irrespective of treatment, 50% of the 236 parasitoids recorded in autumn had a head width measuring 0.430 mm or less, 75% measuring 0.462 mm or less, and 95% measuring 0.616 mm or less (Fig. 1a, autumn), with a range of 0.100–1.792 mm. In autumn, as in spring and summer, nectar was accessible to at least 95% of parasitoids in all three alleyway treatments. With the standard and active management this was provided by three different plant species each. In the standard management, these were the sown species *Mentha suaveolens* and the two unsown species *Solanum nigrum* and *Heliotropium*

europaeum. From the active management, these were the two sown species *M. suaveolens* and *S. verbenaca* and the unsown species *P. aviculare*. *Solanum nigrum* was also present in the control and was the only nectar source available to at least 95% of the parasitoid species (Fig. 1b, autumn).

3.2. Abundance of carbohydrate resources in the alleyways

In all three seasons, the abundance of accessible carbohydrate resource units (nectar and honeydew) in alleyways was found to be significantly affected by alleyway treatment (spring, GLMM: $\chi^2 = 44.21$, $df = 2$, $P < 0.001$; summer, GLMM: $\chi^2 = 31.6$, $df = 2$, $P < 0.001$; autumn, GLMM: $\chi^2 = 9.678$, $df = 2$, $P = 0.008$, $n = 60$) (Fig. 2a and Table B.1.1). In spring, the abundance of carbohydrate resource units in the standard management was 15 times greater than in the control. In summer, both standard management and control alleyways provisioned five times more carbohydrate resource than with active management. In autumn, the standard management provided three times more carbohydrate resource compared to the control.

3.3. Abundance of carbohydrate resources in the tree canopies

All carbohydrate resource units from the canopy were composed of colonies of honeydew-producing hemipterans. In spring and autumn, the abundance of carbohydrate resource in the canopy was affected by alleyway treatment (spring, GLMM: $\chi^2 = 9.2821$, $df = 2$, $P = 0.010$; autumn, GLMM: $\chi^2 = 12.649$, $df = 2$, $P = 0.002$; Fig. 2b). In contrast, no significant difference in carbohydrate resource abundance was found in the canopy in summer (GLMM: $\chi^2 = 5.225$, $df = 2$, $P = 0.073$) (Fig. 2b, Tables B.1.1 and B.1.2). In spring, colonies of honeydew producers were twice as abundant in tree canopies adjacent to alleyways with the standard management compared to the control and active management. No difference was found between the control and the active management. In autumn, colonies of honeydew producers were three times

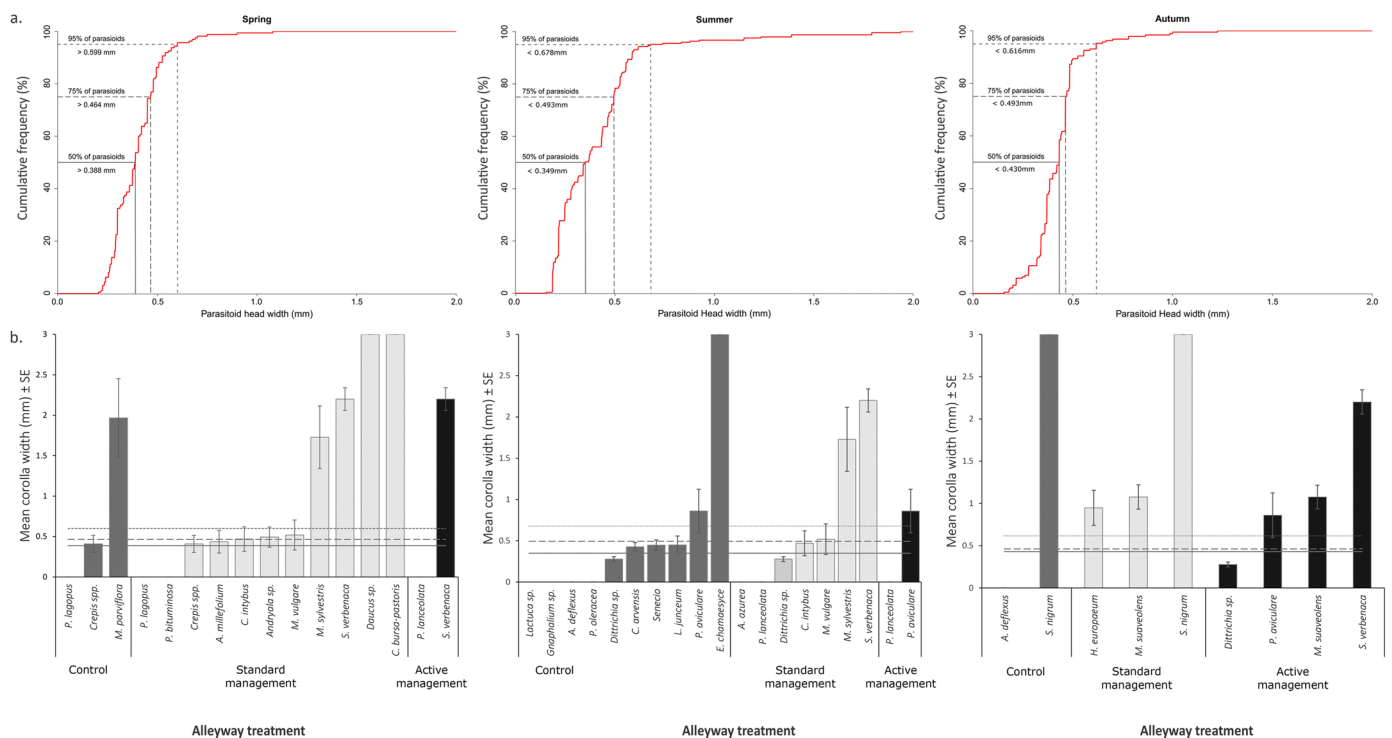
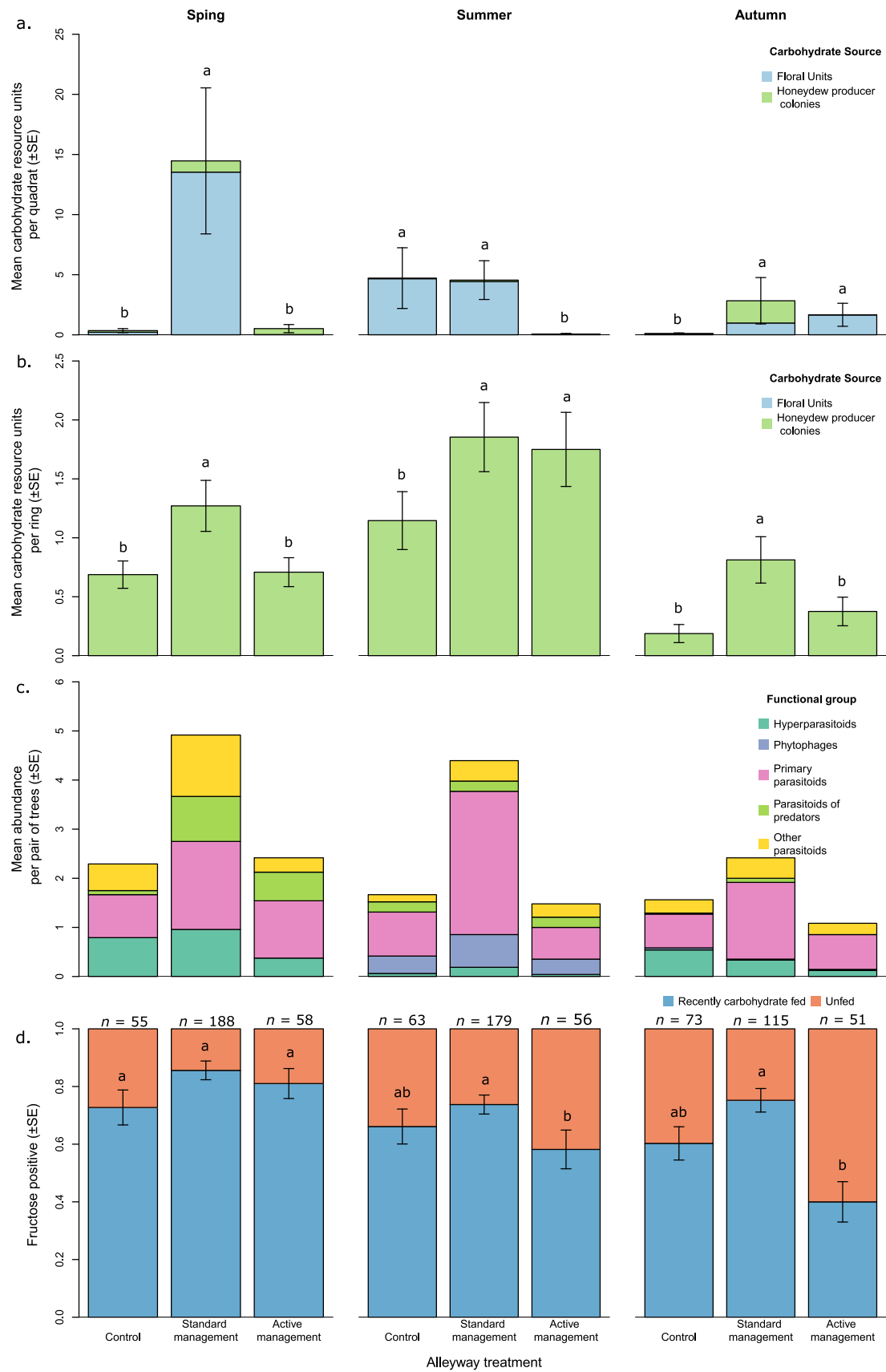


Fig. 1. a) Cumulative percentage of parasitoids of each head width class of 0.001 mm for spring, summer and autumn of 2019 are depicted by the red lines. b) Corolla width measurements of the floral species present in spring, summer, and autumn, for each of the three treatments, control (mid-grey bars), standard management wildflower (light-grey bars), and active management wildflower (dark-grey bars). Error bars represent ± 1 SEM. The parasitoid head width of 50%, 75%, and 95% of sampled parasitoid community are represented by the solid, dashed, and dotted lines, respectively.



(caption on next page)

Fig. 2. The abundance of carbohydrate resource units in a) the alleyways and b) the canopies, according to treatment; control, standard management wildflower and active management wildflower, at the three sampling seasons, spring, summer and autumn of 2019, represented as the mean number of floral units (light-blue bars) and mean number of honeydew-producing hemipteran colonies (light-green bars) per quadrat in the alleyway and per hoop in the canopy (\pm SE). c) The abundances of different trophic functional groups between treatments and across the three seasons (2019). d) The proportion of parasitoids recently fed on fructose (bright-blue bars) and fructose negative (orange-red bars) between alleyway management treatments across the three sampling seasons (2019). Superscripts denotes significance between treatments (Tukey's pairwise contrasts for carbohydrate resource abundance and carbohydrate feeding (a), b) and d)) and Holm's step-down method for functional group abundance (c)); $P < 0.05$.

more abundant in orange trees adjacent to the standard management than in the control and were twice as abundant in the standard management as in the active management.

3.4. Abundance of insect functional groups

Significant differences in the abundances of the five trophic functional groups (primary parasitoids, hyperparasitoids, parasitoids of predators, other parasitoids, and a phytophage) were found between treatments for each season (spring: $\chi^2 = 38.97$, $df = 2$, $P = 0.001$, summer: $\chi^2 = 49.16$, $df = 2$, $P = 0.001$; autumn: $\chi^2 = 26.99$, $df = 2$, $P = 0.007$) (Fig. 2c and Table B.2).

In spring, all functional groups were more abundant in the standard management treatment than the other two treatments (Fig. 2c and Tables B.2.1 and B.2.2). The greatest variation in the model was due to the greater abundance of parasitoids of predators in the standard management (0.92 ± 0.26 individuals per sample) than in the control (0.08 ± 0.06 per sample) and the active management (0.58 ± 0.17 per sample). Other parasitoids were also more abundant in alleyways receiving the standard management (1.25 ± 0.31 per sample) compared to the active management treatment (0.29 ± 0.09 per sample) and the control (0.54 ± 0.13 per sample). Similarly, primary parasitoids were more than twice as abundant in the standard management (1.79 ± 0.33 per sample) than the control (0.88 ± 0.16 per sample) and 50% more abundant in the active management than the control (1.17 ± 0.24 per sample).

In summer, the greatest difference in abundance of the different functional groups was observed between the standard management and the control treatment and the standard management and the active management treatments (Fig. 2c and Tables B.2.1 and B.2.2). These differences between treatments were driven by variation in the abundance of primary parasitoids. Primary parasitoids were three times more abundant in the standard management (2.92 ± 0.48 per sample) than the control (0.90 ± 0.17 per sample) and four times more than in the active management (0.65 ± 0.14 per sample). In summer, the phytophagous species *P. citrella* was captured from the tree canopy, but differences between treatments account for just 4.6% of variation in the model as observed by the test statistics (Table B.2.1).

In autumn, the greatest differences in functional group abundance were observed between the standard management and the control treatment and the standard management and the active management treatments (Fig. 2c and Tables B.2.1 and B.2.2). Primary parasitoids were more than twice as abundant in the standard management (1.56 ± 0.29 per sample) than the control (0.71 ± 0.16) and the active management treatment (0.71 ± 0.15). However, the variation between treatments in autumn was due not only to differences in the abundance of primary parasitoids, but also differences in abundance of hyperparasitoids and parasitoids of predators. Though the abundance of parasitoids of predators was low in the standard management treatment (0.1 ± 0.04 per sample), they were absent from the control and the active management. The abundance of hyperparasitoids in the control (0.6 ± 0.17 per sample) was almost double that of the standard management (0.33 ± 0.11 per sample) and four times that of the active management (0.13 ± 0.06 per sample).

3.5. Fructose feeding in parasitoids

In spring, more than 75% of all parasitoids sampled had recently fed on a fructose source and the proportion of parasitoids which had

recently fed on a fructose source did not differ according to alleyway treatment (GLMM with binomial error structure: $\chi^2 = 4.696$, $df = 2$, $P = 0.096$) (Fig. 2d and Table B.3).

In summer, alleyway treatment was shown to influence the proportion of parasitoids recorded as having recently fed on fructose (GLMM: $\chi^2 = 7.367$, $df = 2$, $P = 0.025$) (Fig. 2 bottom panel and Table B.3). The proportion of parasitoids which had recently fed on fructose in the standard management wildflower treatment was 20% higher than in the active management, but this was not significantly different from the control.

In autumn, the proportion of parasitoids which had recently fed on fructose was also affected by alleyway treatment (GLMM: $\chi^2 = 17.802$, $df = 2$, $P < 0.001$) (Fig. 2d and Table B.3). The proportion of parasitoids which had recently fed on fructose in the standard management wildflower treatment was almost double that of the active management wildflower treatment.

3.5.1. Predicting fructose feeding in parasitoids

The most parsimonious hierarchical GLMM, as selected by dredging in MuMIn, included the following fixed effects: mean carbohydrate resource units in alleyway, parasitoid family, mean corolla width, sward heterogeneity, parasitoid head width, and a two-way interaction between mean corolla width and parasitoid head width (Table 2).

The greater the structural heterogeneity and the larger the parasitoid head width (Fig. 3a), the greater the proportion of fructose-fed parasitoids (Fig. 3b). The proportion of fructose-fed individuals was also different among the 14 parasitoid families identified. Megaspilidae, Ceraphronidae and Platygasteridae showed the highest proportion of fructose-fed parasitoids (Fig. 3c and Table 3).

4. Discussion

The availability of carbohydrate resources for parasitoids in commercial orange orchards was increased by the provision of wildflower strips in alleyways between rows of trees. When managed using the standard wildflower treatment, the structural heterogeneity of the alleyway vegetation was greater which was associated with an increased availability of carbohydrate resources. Of the total carbohydrate sources identified, nectar sources were the most abundant. The standard management wildflower treatment was associated with a greater number of floral units that possessed nectar accessible to parasitoids, which was also provided by a greater number of plant species, compared to the other alleyway treatments. Species included in the wildflower seed mix were selected to provide a range of floral resources throughout the year, and these mixes were further enhanced through the establishment of unsown species. However, regular cutting of alleyways (active management treatment) was associated with a reduction in plant diversity (Mockford, 2021), but also the direct removal of floral resources, and prevented some plants from flowering. Consequently, the standard wildflower management approach was shown to support the greatest abundance of parasitoids, and the highest proportion of parasitoids recently fed on fructose across all three seasons.

In spring, most of the parasitoids collected (>75%) from orange trees across all treatments had recently fed on fructose, suggesting this resource was not limiting regardless of treatment during this season. The proportion of parasitoids which had recently fed on fructose steadily decreased throughout the year in trees adjacent to alleyways receiving the control and active management treatments. This pattern was also

Table 2

Overview of the model selection predicting carbohydrate feeding in parasitoids in orange orchards. The model was fit using the whole parasitoid dataset. Model selection was performed using the dredge function of the MuMIn package in R. The number of parameters in the model is indicated by df, AIC_c is the corrected AIC for small sample sizes, Δ is the difference in AIC_c with the model with the lowest AIC_c value, and Akaike weights (Weight) represent the posterior probability of the model. Based on these parameters, only the ten best models are presented, although any model where Δ < 2 is considered plausible. Terms included in the model are represented by the plus symbol (+) while terms dropped from the model are represented by the minus symbol (-).

Response variable	Model ranked according to weight							
	1	2	3	4	5	6	7	8
Mean abundance of carbohydrate resources units in alleyway	+	+	-	-	+	+	+	+
Family	+	+	+	+	+	+	+	+
Mean corolla width	-	-	+	-	-	+	+	+
Mean abundance of carbohydrate resource units in canopy	-	-	-	-	-	-	-	-
Sward heterogeneity	+	+	+	+	+	+	+	+
Parasitoid head width	+	+	+	+	-	+	+	+
Mean carbohydrate resources units in alleyway * Mean carbohydrate resource units in canopy	-	-	-	-	-	-	-	-
Mean carbohydrate resources units in alleyway * Sward heterogeneity	-	-	-	-	-	-	-	+
Mean carbohydrate resources units in alleyway * Head width	-	-	-	-	-	-	+	-
Mean corolla width * Parasitoid head width	+	-	+	-	-	-	+	+
Mean carbohydrate resource units in canopy * Sward heterogeneity	-	-	-	-	-	-	-	-
df	22	20	21	19	19	21	23	23
AIC _c	857.4	857.9	858.3	858.6	859.2	859.3	859.4	859.5
Δ AIC _c	0	0.498	0.947	1.222	1.781	1.927	2.04	2.08
Weight	0.162	0.126	0.101	0.088	0.066	0.062	0.058	0.057

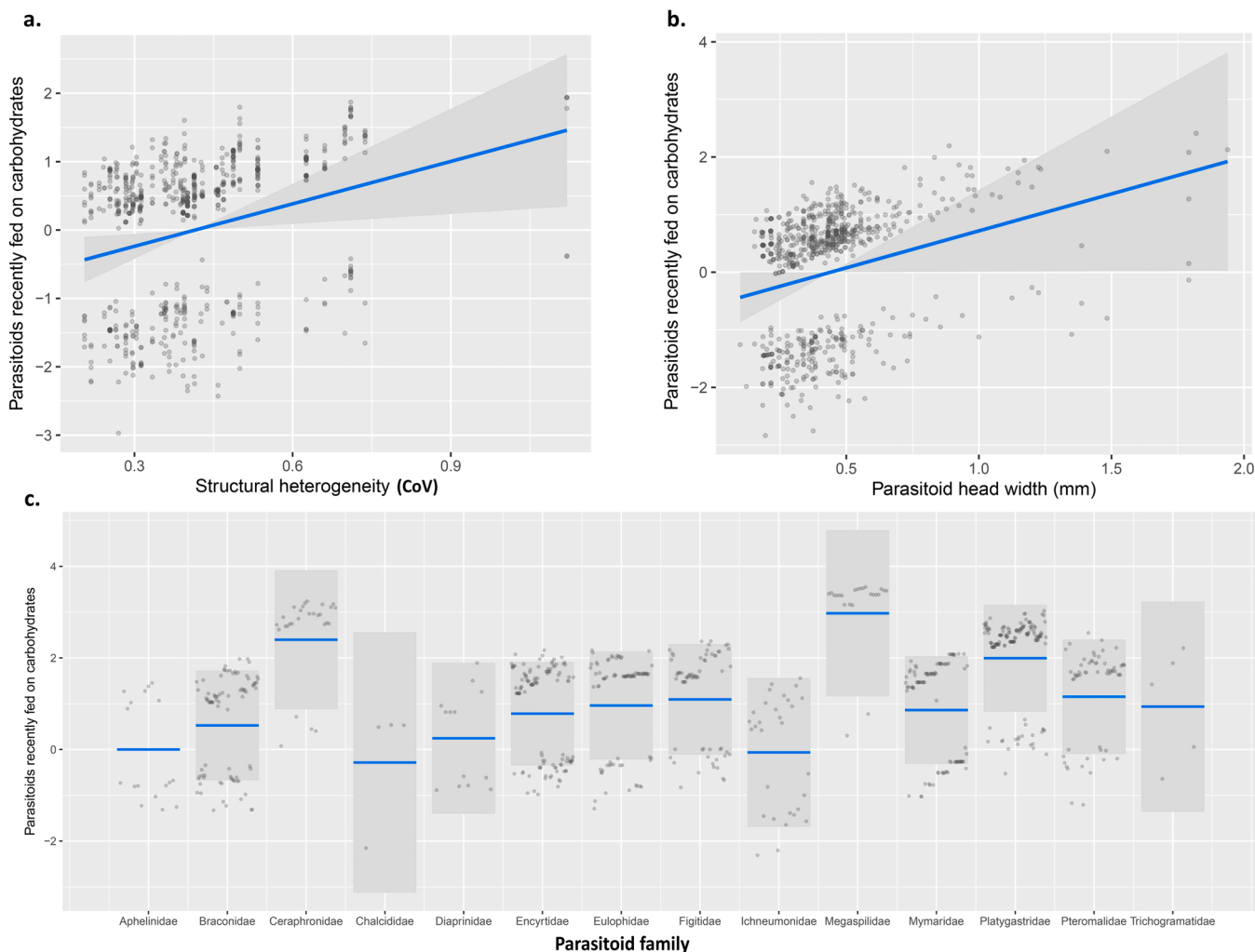


Fig. 3. The effect of each significant independent variable and interaction from the optimal model on parasitoid fructose feeding in field-captured parasitoids (see Table 5.3 for model selection and Table 5.4 for included terms). The fitted lines were predicted from the optimal generalised mixed effects model, the points represent partial residuals, and the grey bands depict confidence intervals. Plots were generated using the visreg and ggplot2 packages in R.

Table 3

Model estimates and 95% confidence intervals (on a natural logarithm scale) of the most parsimonious model (model 1, Table 2) predicting carbohydrate feeding in parasitoids in orange orchards and based on parasitoids and orchard characteristics. The model has an AIC of 856.0 (AICc = 857.4) and a binomial error distribution.

Predictors	Odds Ratios	Lower 95% CI upper	Lower 95% CI upper	P-value
(Intercept)	0.40	0.14	1.12	0.081
Mean carbohydrate resources units in alleyway	1.01	0.99	1.03	0.349
Braconidae	0.63	0.36	1.08	0.092
Ceraphronidae	3.97	1.37	11.49	0.011*
Chalcididae	0.36	0.03	3.96	0.407
Diapriidae	0.50	0.16	1.55	0.229
Encyrtidae	0.72	0.44	1.19	0.199
Eulophidae	1.20	0.69	2.11	0.517
Figitidae	1.16	0.63	2.16	0.633
Ichneumonidae	0.41	0.15	1.12	0.081
Megaspilidae	5.99	1.47	24.44	0.013*
Mymaridae	0.84	0.44	1.61	0.594
Platygastridae	2.63	1.49	4.64	0.001**
Pteromalidae	1.13	0.60	2.14	0.709
Trichogrammatidae	0.95	0.15	6.13	0.958
Mean corolla width	1.43	0.97	2.11	0.072
Sward heterogeneity	9.93	2.49	39.59	0.001**
Parasitoid head width	5.04	1.34	18.96	0.017*
Mean corolla width * Parasitoid head width	0.46	0.21	1.00	0.050

observed by Tena et al. (2015) in orchards sown with only the grass species *Schedonorus arundinaceus*. In contrast, wildflower strips containing a range of different nectar-producing species left uncut from February each year (standard management) prevented this seasonal decline and supported fructose feeding in parasitoids across all three seasons. According to the 'nectar provision hypothesis', the standard management wildflower treatment might therefore be expected to enhance pest regulation services in commercial orange orchards (Heimpel and Jervis, 2005).

The study has demonstrated the importance of promoting not only the provision of nectar but also the structural heterogeneity in wildflower strips to boost fructose feeding in parasitoids. Structural heterogeneity can be an indicator of accessibility into the sward, facilitating foraging by arthropods within otherwise dense habitats. Structural heterogeneity within the wildflower strips can be enhanced by increasing not only the number of plant species, but also plant trait and functional group diversity (Woodcock et al., 2007). Increased structural heterogeneity in alleyways can therefore be achieved by establishing wildflower strips with a diverse range of native plant species from distinct functional groups, such as the tussock-forming grasses *Dactylis glomerata* and *Schedonorus arundinaceus*, the low growing forbs *Salvia verbenaca* and *Plantago lanceolata*, and the tall woody forbs *Cichorium intybus* and *Psoralea bituminosa*. Additionally, management practices applied to perennial wildflower strips can create germination niches and promote heterogeneity, especially in older swards which may become more homogenous over time (Westbury et al., 2017).

The total abundance of insect functional groups was consistently greater from the canopy with standard management wildflower treatment than the control or active management treatments, though the responses of the different functional groups varied across treatments and seasons. The standard management wildflower treatment increased the abundance of primary parasitoids but not hyperparasitoids in summer and autumn. Both functional groups fed similarly on fructose, therefore, other resources provided by the standard management wildflower strips, such as alternative hosts, refuge, and shelter against adverse climatic conditions, might have favoured primary parasitoids (Rand et al., 2012). Greater structural heterogeneity can reduce competition between

species in the third trophic level, such as primary parasitoids (Chesson, 2000). For example, in simple homogeneous habitats, competition for a shared resource between members of the third trophic level is increased as phytophage diversity and abundance is limited (Woodcock et al., 2009, 2007). Additionally, as higher trophic levels, such as hyperparasitoids, require a greater complexity of cues to successfully locate foraging patches, wildflower strips of high structural heterogeneity may impede patch identification (Aartsma et al., 2019). Therefore, increased structural heterogeneity in the standard management wildflower treatment might present more foraging opportunities for primary parasitoids under relaxed competition. Further empirical evidence is necessary to explain what causes the differences between these two parasitoid functional groups. Nevertheless, this finding is of significance for biological control as other authors have also expressed caution of feeding hyperparasitoids through the provision of nectar intended for primary parasitoids (Pinheiro et al., 2019; Tougeron and Tena, 2019).

Ten different plant species found in the alleyways of orange orchards were found to possess nectar that was accessible to 95% of the parasitoid community. However, of these only two species were sown (*Mentha suaveolens* and *Salvia verbenaca*), and the other eight species were unsown. Five of these ten species provided nectar for parasitoids in spring (*Capsella bursa-pastoris*, *Daucus* sp., *Malva parviflora*, *Malva sylvestris*, and *Salvia verbenaca*), compared to three in summer (*Euphorbia chamaesyce*, *M. sylvestris*, *Polygonum aviculare*, and *S. verbenaca*), and five in autumn (*Heliotropium europaeum*, *Mentha suaveolens*, *P. aviculare*, *S. verbenaca*, and *Solanum nigrum*). Importantly, the sown species *S. verbenaca* was the only species present throughout all three seasons that provided accessible nectar for 95% of parasitoids. *Heliotropium europaeum* and the sown species *M. suaveolens* provided an accessible resource for parasitoids during autumn, when carbohydrate availability can be limiting for parasitoids in citrus (Tena et al., 2013b). However, not all plant species were consistently recorded at all sites. For example, *M. suaveolens* was only present at two of the three sites. Similarly, *H. europaeum* was only found at two sites, and only in association with the standard management treatment.

The unsown species *P. aviculare* allowed access to 95% of the parasitoid community and has nectar of high quality for parasitoids (Russell, 2015) but is a highly competitive annual, able to suppress the establishment of other species (Alsaadawi and Rice, 1982). Nonetheless, as it was found across all sites, it might be an important unsown carbohydrate resource for parasitoids which can be expected to establish in Mediterranean wildflower strips (Benelli et al., 2014). *Polygonum aviculare* is associated with high disturbance (Costea and Tardif, 2005) and was most common in the two treatments characterised by regular cutting, the control and active management wildflower treatment. As such, there would be no need to sow this species, instead management strategies aimed at increasing structural heterogeneity, such as patch scarification which can provide germination niches (Westbury et al., 2008), could be used to boost this species if required.

Despite providing nectar and extrafloral nectar (Gentry, 2003), *S. nigrum* is associated with diverse acarifauna and can harbour economically important citrus pest species, such as *Tetranychus urticae* Koch (Acari: Tetranychidae) (Aucejo et al., 2003; Celepci et al., 2017; Ferreira and Sousa, 2011). However, it can also support populations of non-pest mite species and mite predators that might move into the citrus canopy (Aucejo et al., 2003; Pereira et al., 2014). Similarly, although *Malva* species can host a diverse range of aphid species which provide accessible honeydew to parasitoids, they can also host the citrus pest *Aphis gossypii* Glover (Hemiptera: Aphididae). *Psoralea bituminosa* and *A. millefolium* did not have accessible nectar for most parasitoid species but hosted hemipteran species that excrete honeydew during autumn. The roots of these two plant species harboured colonies of *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) and *Coccus hesperidum* L. (Hemiptera: Coccidae), respectively. These species excrete honeydew of high quality for parasitoids, but they can also inflict economic damage in citrus (Tena et al., 2013a). Further investigation is required to determine

the potential risks or benefits these species might represent to citrus growers, especially in the standard management, where the abundance of honeydew producers was higher.

5. Conclusions

To enhance pest regulation services in Mediterranean orange orchards by supporting fructose feeding in primary parasitoids the management of sown wildflower strips should focus on the promotion of high structural heterogeneity. A diverse range of native plant species with distinct functional traits, such as tussock forming grasses, low growing forbs, and tall woody forbs, should therefore be included in sown seed mixes. The wildflower strips should then be managed by cutting just once per year, this increases nectar availability and supports fructose-feeding which otherwise decline throughout the seasons. Based on their accessibility to a high proportion of parasitoids (>95%) and ubiquity across seasons, three forb species, the sown *S. verbenaca* and *M. suaveolens*, and the unsown *H. europaeum*, are recommended.

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

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.108139](https://doi.org/10.1016/j.agee.2022.108139).

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