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Sugar feeding of parasitoids in an agroecosystem: effects of community composition, habitat and vegetation

MIRIAM KISHINEVSKY,¹ NITZAN COHEN,² ELAD CHIEL,² ERIC WAJNBERG^{3,4} and TAMAR KEASAR² ¹Department of Evolutionary and Environmental Biology, University of Haifa, Haifa, Israel, ²Department of Biology and Environment, University of Haifa – Oranim, Tivon, Israel, ³INRA, Sophia Antipolis Cedex, France and ⁴INRIA – Sophia Antipolis – Projet Hephaistos, Sophia Antipolis Cedex, France

Abstract. 1. Sugar from nectar or from honeydew can prolong parasitoids' lifespan, enhance their fecundity and foraging ability, and thereby increase their pest suppression efficiency. Sugar sources within crop monocultures are considered to be limiting for parasitoids. Nevertheless, only few studies have measured the sugar feeding of parasitoid assemblages in agricultural areas or in surrounding non-crop habitats.

2. We used cold anthrone tests to compare the frequency of sugar feeding in parasitoid communities, inside pomegranate orchards and in adjacent natural areas, over two consecutive years. Overall, 40% of the 1610 sampled individuals belonging to 135 species scored positive for sugar.

3. Sugar-feeding frequency was lower within the orchards than in the neighbouring natural areas. The proportion of sugar-fed wasps increased with herbaceous vegetation cover, both within and outside the orchards, suggesting that herbs are a sugar-rich habitat. Parasitoids sampled from trees and from herbs within the orchards had similar frequencies of sugar feeding, despite differences in wasp species composition.

4. Our results probably overestimate sugar-feeding frequencies in the field because sugar-fed individuals have higher longevity and hence are more likely to be sampled. We propose a simple model to approximate this over-sampling bias and apply it to *Encarsia inaron* (Aphelinidae), one of the most abundant parasitoids in the samples.

5. We conclude that sugar availability potentially limits parasitoid fitness in this agro-ecosystem. This may be due to the low density of plants in natural areas during the Mediterranean summer, and to herbicide applications within the orchards that further suppress non-crop herbs.

Key words. Cold anthrone test, *Encarsia inaron*, honeydew, nectar, sugar feeding.

Introduction

Modern agricultural areas are usually characterised by low plant diversity in comparison to natural landscapes, because of intensive weed control (Matson *et al.*, 1997). These agricultural monocultures often suffer greatly from pest outbreaks that lead to intense pesticide use (Andow 1991; Knops *et al.*, 1999; Haddad *et al.*, 2011). One of the possible reasons for pest outbreaks is that natural enemies may lack non-host/prey resources in the agricultural areas, which might reduce their effectiveness in biological control (Landis *et al.*, 2000; Parker *et al.*, 2013; Begg

Correspondence: Miriam Kishinevsky, Department of Evolutionary and Environmental Biology, University of Haifa, Tivon 36006, Israel. E-mail: mashakish@gmail.com

et al., 2016). Most adult parasitoids, for example, benefit from sugar feeding (Casas et al., 2003; Heimpel & Jervis, 2005; Lee & Heimpel, 2008) and actively search for sugar sources in the field (Jervis et al., 1993; Desouhant et al., 2010). Sugar, mainly in the form of floral nectar or honeydew (Heimpel et al., 2004), can indeed dramatically prolong adult parasitoid lifespan, enhance females' fecundity and increase their foraging abilities, allowing them to lay more eggs and thereby provide better pest control (Lewis et al., 1998; Siekmann et al., 2001; Winkler et al., 2006; Tena et al., 2015). Most parasitoids were found to feed on sugar in laboratory settings, and Jervis et al. (1993) observed around 250 parasitoid species from 15 Hymenopteran families feeding on flower nectar in the field. Following these findings, flowering plants are added to agricultural fields of several crop types in some parts of the world as a measure of conservation biological control (Landis et al., 2000; Parker et al., 2013). Sugar may, however, not be a limiting factor in all agricultural areas. Potential sugar-rich sources include honeydew produced by sap-feeders, natural flowering vegetation growing in the margins of the plot and, especially in the case of orchards, flowering herbs growing in between the tree rows that provide nectar to parasitoids (Heimpel & Jervis, 2005). In addition, sugar sources could promote the activity of hyperparasitoids and thereby reduce the efficiency of primary parasitoids as natural enemies of pests (Araj et al., 2008; Harvey et al., 2012).

Due to the complexity of the system and the usually small size of parasitoids, sugar feeding in agricultural and natural settings remains poorly understood. Sugar feeding was studied under field conditions in a few parasitoid species only, and sugar-feeding frequencies seem to vary greatly among sites, species and seasons (Lee & Heimpel, 2003; Heimpel *et al.*, 2004; Lee *et al.*, 2006; Segoli & Rosenheim, 2013).

In this study we asked whether adult parasitoids feed on sugar sources in pomegranate orchards during the hot and arid Mediterranean summer, and whether the natural areas in the vicinity of the orchards can provide more sugar resources than the orchards themselves. We compared the sugar-feeding proportion of parasitoid assemblages sampled on the pomegranate trees to parasitoids found on herbs inside the orchard and to those found in the natural areas around the orchards. We also tested whether the species composition of the parasitoid assemblages differs between the natural and agricultural areas, because such differences could also affect the communitylevel sugar feeding frequencies.

Materials and methods

Study sites and sampling protocol

Six orchards from different geographic regions in Israel were sampled in June 2015 and eight orchards were sampled in August 2016 (see Table S1; Fig. S1). Samplings took

place during the summer since it is the pomegranate fruit growth season and a period of high insect activity. The season is characterised by high mean temperatures (25–27 °C), no rainfall and little blooming of the local wild plants (Keasar & Shmida, 2009). All orchards had a naturally growing vegetation area that bordered one of the sides of the plot. Arthropods were sampled from the herbs growing inside the orchards, and from the natural vegetation adjacent to the orchards. In addition, pomegranate trees from the centre of the orchards were sampled in the second year of the study. Since the hour of the day can influence the proportion of sugar feeding (Lee & Heimpel, 2003; Segoli & Rosenheim, 2013), the samples in the plots and the natural areas around them were taken no more than half an hour apart. Arthropods were sampled by vacuuming (Vortis Insect Suction Sampler, Burkard Manufacturing Co. Ltd, Rickmansworth, UK) for 30 s. The samples were collected from five 3-m transects at haphazardly selected locations (for vegetation samples from the orchards and the natural areas) or along three trees (for pomegranate tree samples). and immediately placed on ice to inhibit sugar digestion. They were then transported to the lab and stored at -35 °C until identification of species and sugar-feeding status. Sampled plants were identified to the species level in the field using Danin and Feinbrun-Dothan (1991) key. The percentage cover of green plants at each sampling location was visually estimated and agreed upon by the team of three field workers. In 2016 we also recorded which of the sampled plant species were flowering.

Parasitoid identification

All collected parasitoid wasps were classified morphologically to morphospecies while cooled with ice. All individuals were identified at least to the family level; most were identified to genera and some to species. Classification was done based on Goulet and Huber (1993); Gibson *et al.* (1997); Hayat (1983); Huber *et al.* (2009); Masner (1976, 1980); Noyes (2003); Pinto (2006); Pricop (2013); Schauff *et al.* (1997); Shaw and Huddleston (1991); Ulrich (2006); and Woolley (1997).

Gut sugar analysis

To determine whether sugar was present in the gut of the captured parasitoids a qualitative cold anthrone test was performed (Van Handel, 1985; Heimpel *et al.*, 2004). After identification to morphospecies, parasitoids were mounted individually on a microscope slide, a drop of cold anthrone was placed directly on each parasitoid and a covering glass was positioned on top. The covering glass was gently pressed to tear the body of the wasp and allow the gut content to spill. The slide was checked for a colour change (blue-green), which indicates the presence of fructose. The colour reaction usually occurs within 15 min, but occasionally requires more time. Therefore,

colour changes were recorded for up to an hour after anthrone application (Heimpel *et al.*, 2004). A subset of the colour scores were verified by an additional observer. In 2016, all slides were photographed within 1 h of the test to allow later verification of the colour score. The photos are available on request from the corresponding author.

Modelling the population-wide frequency of sugar feeding

The proportion of anthrone-positive responses among the sampled individuals might be an over-estimate of the fraction of the wasp population that had fed on sugar in the field. This is because sugar-fed individuals often survive longer and thus are more likely to be sampled. While this bias should not affect the comparison of sugar-feeding rates between habitats, it implies that the populationwide sugar feeding frequency is probably lower than the estimate based on the anthrone tests. The magnitude of the over-estimate can be approximated using the following simple static model:

MF and MH represent the daily mortality risks of sugar-fed and sugar-hungry wasps respectively $(0 < MF < MH \le 1)$. SF and AP represent the frequencies of sugar feeding in the entire surviving wasp community and of anthrone-positive scores in the sampled wasps respectively. In an equilibrium wasp community, where mortality equals birth, AP is the fraction of the sugar-fed, surviving wasps out of the total surviving population. The numerator of the fraction expresses the probability of both sugar-feeding and surviving, SF(1 - MF). The denominator expresses the probability of either sugar-feeding and surviving SF(1 - MF) or remaining sugar-hungry and surviving (1 - SF)(1 - MF). Thus:

$$AP = \frac{SF(1 - MF)}{SF(1 - MF) + (1 - SF)(1 - MF)}$$
(1)

which can be rearranged to estimate SF:

$$SF = \frac{AP(1 - MH)}{1 - MF + AP(MF - MH)}$$
(2)

Data analysis

A mixed generalised linear model (GLMM) for binomial data with a logit link function was used to test the effects of habitat type, green vegetation coverage percentage and year on the positive/negative anthrone response. Habitat type was defined as either natural vegetation, vegetation within the orchard, or (in 2016 only) pomegranate tree. Vegetation cover was affected by habitat type (see Results). Therefore, we used the residuals of this relationship in the GLMM, so as to test for the effect of vegetation cover percentage after removing the influence of habitat type. Habitat and the residual vegetation cover were defined as fixed factors in the model, while year and sampling site were defined as random-intercept factors. The interaction between habitat type and sampling site was also tested by including it as a random-slope factor. Using likelihood ratio tests, we compared this full GLMM model with three reduced models, in which we consecutively excluded effects of habitat type, residual vegetation cover and year as explanatory variables. This allowed us to test the effect of each variable separately on the anthrone response. After finding a significant effect of habitat, Tukey's post-hoc tests were performed to test which of the three habitats sampled in 2016 were different from the others. Most species did not occur in all combinations of year, site and habitat. This resulted in many missing values that did not allow testing for the effect of species in the GLMM. Nonetheless, differences in sugar feeding frequencies between habitats may actually reflect differences in the species composition of the tested parasitoids, or in the composition of their food plants. To evaluate these possibilities, we compared the species assemblages using 'Adonis' (PERMANOVA) analyses (Anderson, 2001), a nonparametric version of multivariate analysis of variance (MANOVA). The data of 2015 and 2016 were analysed separately. In 2015, we compared the composition of plant species and parasitoid morphospecies between agricultural and natural habitats. In 2016, we considered two habitats (agricultural or natural) for the plant communities, and three habitats (orchards trees, orchard herbs or herbs in nature) for the parasitoid communities. We performed two pairwise comparisons of the 2016 parasitoid communities (orchard trees vs. herbs, and orchard herbs vs. herbs in nature), because post-hoc tests are not available for the 'Adonis' procedure. We used the Bonferroni correction for multiple testing for these comparisons and thus considered 0.05/2 = 0.025 as the significance threshold level. The data were stratified according to location to account for the paired structure of the samples.

All statistical analyses were conducted in R version 3.1.2 (R Core Team 2013). The packages 'lme4' (Bates *et al.*, 2014), 'vegan' (Oksanen *et al.*, 2007) and 'mult-comp' (Hothorn *et al.*, 2008) were used for the GLMMs, Adonis tests and *post-hoc* test respectively.

Results

Parasitoid sample sizes

Altogether, 800 and 810 parasitoids were sampled in 2015 and 2016 respectively. Habitats with fewer than ten parasitoids were excluded (Giv'at Haim pomegranate tree and Hazor herbs inside the orchard in 2016).

Parasitoid sugar-feeding scores

Anthrone-positive scores were significantly affected by habitat (GLMM, $\chi^2_2 = 7.17$, P = 0.027). Tukey's *post-hoc*

tests showed that anthrone-positive responses were higher in the natural vegetation than in the orchard's herbaceous vegetation and trees (Z = 3.08, P = 0.006, Z = 2.50, P = 0.024 respectively) but similar in the pomegranate trees and on the herbs beneath them in 2016 (Z = -0.94, P = 0.35, Fig. 1). The proportions of anthrone-positive wasps were 0.26 in 2015 and 0.55 in 2016, for all parasitoids pooled. This is reflected in a significant effect of year on the anthrone response ($\chi^2_1 = 6.15$, P = 0.013, Fig. 1). The anthrone-positive response increased with vegetation cover (Fig. 2). Herbaceous vegetation cover was higher in the natural areas (mean and SE: $80.4 \pm 1.2\%$) than within the orchards (27.95 $\pm 0.85\%$), and thus was significantly influenced by habitat (GLM: $F_{2.1566} = 649.8$, P < 0.001). We eliminated the effect of



Fig. 1. Proportions (means \pm SE) of anthrone positive parasitoids in the different habitats. Columns marked by * differ significantly (P < 0.05). NS, non-significant difference.



Fig. 2. The proportion of anthrone positive parasitoids plotted against the percent cover of green vegetation. Each data point represents a habitat (orchard or natural habitat) in one of the study sites. Percent vegetation cover was not recorded for one of the 2016 sites (Ramot – natural habitat), and parasitoid sample size was <10 in one of the habitats of a second site (Hazor), hence data are plotted for 13 sites only.

habitat on vegetation cover in the GLMM by replacing the vegetation cover variable with the residuals of the vegetation cover-by-habitat model. This revealed a significant effect of vegetation cover *per se* on the anthrone response $(\chi^2_1 = 8.37, P = 0.004)$.

To roughly estimate the bias due to oversampling of sugar-fed individuals, we used Eqn (2) to approximate the population-level sugar-feeding (SF) rate of Encarsia inaron (Aphelinidae), one of the most common species in our samples (see Table 1 for abundance data). The congener E. formosa (which was not present in our samples) has a maximal lifespan of 5 days when water-fed, and 18 days when fed with glucose (Hirose et al., 2009) under laboratory conditions. We converted these value to daily mortality rates and used them as mortality estimates, MH = 0.6 and MF = 0.2, for hungry and fed wasps The proportion of anthrone-positive respectively. E. inaron out of all sampled individuals (AP) is 0.22 (Table 1). Based on these parameter values, the estimated population-level sugar feeding rate of E. inaron can be as low as 0.12.

Parasitoid and plant community composition

All genera collected were primary parasitoids, except for five individuals of the hyperparasitoid genus Alloxysta that were collected in 2015. We tested whether the composition of parasitoid and plant species differs among habitats, because such differences (if found) may explain the higher sugar feeding frequencies in the natural areas. Tree and herb communities were indeed dominated by different wasps: in both years, the genus Telenomus (Platygastridae) was dominant on the herbaceous vegetation, both inside the orchards and in the wild areas. This genus, represented by a few morphospecies, accounted for 35.7% and 15.1% of the sampled parasitoid in 2015 and 2016 respectively. Different parasitoids dominated the pomegranate trees: 35% of the wasps were of the species Encarsia inaron and 20% were of the genus Barvscapus (Eulophidae) (Table 1).

These trends are reflected in the PERMANOVA analysis as well: Parasitoid community composition on the herbaceous vegetation was similar in the natural areas and inside the orchards in both years (2015: Adonis: $F_{1,10} = 0.69$, $r^2 = 0.064$, P = 0.687; 2016: Adonis: $F_{1,13} = 0.65$, $r^2 = 0.047$, P = 0.937).Community composition on the pomegranate trees, however, which were sampled in 2016, differed from that of the other two habitats (pomegranate trees compared with the vegetation inside the orchards and in the wild – Adonis: $F_{1,20} = 2.84$, $r^2 = 0.11$, P = 0.003).

Plant community composition was also similar between the orchards and the natural areas in 2015 (Adonis: $F_{1,8} = 1.11$, $r^2 = 0.12$, P = 0.25). In 2016, however, a significant difference was found between the habitats (Adonis: $F_{1,14} = 1.78$, $r^2 = 0.11$, P = 0.023). For plant species and their flowering status (see Table S2).

Table 1.	Abundance	of the	parasitoid	morphospecies	(listed	alphabetically	and	pooled	over	all site	es) in	the	suction	samples	and	propor-
tions of a	anthrone-posi	itive re	sponses.													

	2015				2016							
	Abund	ance		A 41	Abundance							
Parasitoid morphospecies	Wild areas	Wild Herbs in areas orchards		positive proportion	Wild areas	Herbs in orchards	Pomegranate trees	Total	positive proportion			
<i>Aphelinoidea</i> sp. (Trichogrammatidae)	13	7	20	0.05	2	0	0	2	_			
(Eulophidae)	4	5	9	_	21	16	51	88	0.61			
<i>Encarsia inaron</i> (Aphelinidae)	0	1	1	_	2	5	92	99	0.22			
<i>Encarsia lutea</i> (Aphelinidae)	0	0	0	_	10	12	1	23	0.26			
<i>Eretmocerus</i> sp. (Aphelinidae)	0	0	0	_	3	9	14	26	0.29			
<i>Lymaenon</i> sp. (Mymaridae)	140	17	157	0.14	24	2	1	27	0.91			
<i>Neochrysocharis</i> sp. (Eulophidae)	2	6	8	_	9	11	0	20	0.3			
<i>Oligosita</i> sp. (Trichogrammatidae)	6	7	13	_	9	4	0	13	_			
<i>Platygastrinae</i> sp. (Platygastridae)	10	0	10	_	23	17	0	40	0.57			
Polynema sp. (Mymaridae)	64	7	71	0.05	3	2	0	5	_			
Telenomus sp.1 (Platygastridae)	0	0	0	_	21	0	0	21	0.76			
Telenomus sp.2 (Platygastridae)	0	0	0	_	3	7	22	32	0.37			
Telenomus sp.3 (Platygastridae)	160	85	245	0.28	8	19	28	55	0.7			
<i>Telenomus</i> sp.4 (Platygastridae)	26	13	39	0.41	14	11	10	35	0.89			
<i>Telenomus</i> sp.5 (Platygastridae)	21	7	28	0.5	7	8	1	16	_			
<i>Ufens</i> sp. (Trichogrammatidae)	0	0	0	_	22	8	1	31	0.61			
Fewer than 20 individuals in both years combined	134	65	199	_	125	113	39	277	_			
All individuals	580	220	800	0.25	306	244	260	810	0.55			

The proportions of anthrone-positive were calculated for morphospecies represented by >20 individuals. Parasitoids were identified to genera and to species or morphospecies except for one species of Platygastrinae that was identified to sub-family. Five common morphospecies were sampled from the genus *Telenomus* and were assigned arbitrary identification number.

Discussion

The central finding of our study is that parasitoids' sugar feeding in pomegranate orchards are significantly lower than in the surrounding natural areas (Fig. 1). This result agrees with the hypothesis that non-host resources in agricultural areas might be limited, which may reduce the fitness of natural enemies and thus their efficiency as biological control agents (Landis *et al.*, 2000; Parker *et al.*, 2013; Begg *et al.*, 2016). Similar low levels of sugarfeeding in agricultural habitats, especially towards the end of the season when adjacent vegetation was dry, were

reported by Segoli and Rosenheim (2013) who monitored *Anagrus* parasitoids (Hymenoptera: Mymaridae) within vineyards in northern California, USA. On the other hand, Lee and Heimpel (2003) and Lee *et al.* (2006) reported a higher feeding proportion in cabbage fields (more than 60%). This difference can result from the buckwheat flowers added in the margins of the plots in the latter two studies or from the different insect sampling method used.

Parasitoid composition was similar in the vegetation inside the orchards and in the natural areas. This indicates that the different sugar-feeding proportions in the two

habitats were probably not due to specific parasitoid species requiring fewer sugar meals in the orchards. The parasitoid community on the trees, however, differed from those found in the herbaceous vegetation, both beneath the trees and in the natural areas. Therefore, the possibility that specific parasitoids found on the trees are responsible for the low sugar-feeding rates cannot be ruled out. Nonetheless, the almost identical sugar-feeding rates found on the pomegranate trees and in the vegetation beneath them may indicate that all parasitoids inside the agricultural plot exploit similar resources, and that these resources are less abundant than in natural habitats. Moreover, the proportion of anthrone-positive individuals varied greatly between years within the same habitats for some of the species. For example, in one of the common morphospecies of the genus Telenomus, the proportion of sugar-positive wasps increased from 28% in 2015 to 70% in 2016 (Table 1). In this case (and possibly also in others), the lower sugar-feeding rate in 2015 is probably the result of resource limitation.

Parasitoids get sugar meals mainly from floral and extrafloral nectar, hemipteran honeydew or fruit juices (Heimpel et al., 2004). In the present study, the source of the sugar found in the sampled parasitoids could not be identified. Parasitoids may feed in wild areas and migrate into agricultural plots to find their hosts. Parasitoids can digest a sugar meal within a few days (Heimpel et al., 2004) and it is likely harder for them to find another meal inside agricultural plots. Feeding was positively correlated with the percentage of green herbaceous vegetation cover (Fig. 2), which indicates that parasitoids may find sugar on the plants. Since parasitoids were sampled during the hot and dry Mediterranean summer, there were not many flowering plants around. Nonetheless, some plant species were flowering (Table S2) and could be the source of the sugar found within the parasitoids' guts. Application of herbicides inside the orchards reduces herb populations and probably also the sugar resources that they provide. This might be the reason for lower frequency of sugar feeding in the agricultural plots. Although certain floral nectar was found to be more nutritious than honeydew for some parasitoids (Lee et al., 2004; Wäckers et al., 2008), it is also possible that green vegetation cover provides habitats for honeydew-producing insects. Even parasitoids that develop on other hosts could exploit the honeydew as a sugar source (Tena et al., 2013b). It is, however, important to acknowledge that honeydew-secreting whiteflies, leafhoppers and aphids often infest pomegranate trees during the summer in Israel and nonetheless sugar-feeding on the trees was lower than in the natural habitat. This could be explained by the intensive insecticide usage in the orchards that reduces hemipteran numbers compared with their populations in the wild.

Some parasitoids may have lower feeding requirements than others (Heimpel & Jervis, 2005). For example, Hardy *et al.* (1992) found that *Goniozus nephantidis* (Hymenoptera: Bethylidae) lifespan is not prolonged when fed on honey compared with starved individuals. Differences in sugar requirements cannot account for the lower feeding proportion on vegetation inside the agricultural plots because the wasps' community composition in our study appears similar in both habitats. The presence of species with low sugar requirements could, however, explain the overall low feeding rates. We were not able to test this possibility directly, by comparing per-species sugar feeding in different habitats, because most sampled species were not sufficiently represented across habitats and locations. To determine whether sugar sources are limited in the wild as well, sugar sources should be experimentally added. A higher sugar feeding rate under food supplementation would indicate that resources were insufficient in our study sites. In addition, Tena et al. (2013a) showed a high variability among the qualities of the honeydew produced by different hemipterans and therefore some of the parasitoids that tested positive for sugar feeding could gain less fitness than others.

The most abundant parasitoid found on the pomegranate trees was Encarsia inaron (Table 1). This species is a natural enemy of the ash whitefly (Siphoninus phillyreae) (Hemiptera: Aleyrodidae) (Noyes, 2003), a key pest that occasionally infests the orchards in Israel. In 2016, the farmers in the sampled areas reported a severe outbreak of the pest which can explain the high numbers of E. inaron. Encarsia inaron was found to have a low sugar-feeding proportion - less than a quarter of the individuals were anthrone-positive. After sampled accounting for the probable oversampling of anthronepositive individuals, we estimate the population-wide sugar feeding rate to be even lower. Similar to our findings, other members of the Aphelinidae family were also reported to have low sugar feeding levels in the field (Heimpel et al., 2004; Heimpel & Jervis, 2005). Encarsia inaron females are known to host-feed (Gould et al., 1995) and, therefore, it is unclear whether this key natural enemy is limited by sugar availability, and thus whether it can benefit from provisioning of additional sugar sources in the orchards. This could be the case for other species as well.

Our simple model, aimed to correct sugar-feeding estimates for oversampling of fed wasps, provides a useful first approximation of the possible sampling bias. It is limited, however, in assuming a fixed daily mortality rates and by deriving mortality parameters from laboratory studies. To improve the model, survival curves of fed and unfed individuals under field conditions would be needed. As far as we are aware, these data are not yet available for any parasitoid species. Further studies on this topic are warranted.

In conclusion, the present work supports the hypotheses that resources for natural enemies in agricultural areas are restricted, and that green non-crop vegetation can support parasitoids in agro-ecosystems. More research is needed to understand the dynamics of parasitoid sugar feeding, and whether our findings are applicable to areas and seasons that are less arid.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/ icad.12259:

Figure S1. A map of the sampling sites, based on Google maps.

Table S1. Details of the pomegranate orchards participating in the study.

Table S2. (a) Plants recorded in pomegranate orchards and the natural areas around them in (a) 2015 (listed alphabetically) and (b) 2016 (listed alphabetically).

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