

Parasitoid abundance on plants: effects of host abundance, plant species, and plant flowering state

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Abstract The abundance of parasitoids on plants that harbor their monophagous herbivorous host often correlates with host numbers. However, when hosts are polyphagous, the species-specific characteristics of the plants can affect parasitoid abundance as well. We asked whether parasitoids that attack a polyphagous host aggregate on individual plants with high host densities, and whether plant-related factors (plant species and flowering state) also account for the parasitoids' abundance on the plants. We sampled *Encarsia* (Förster) (Hymenoptera: Aphelinidae) parasitoids and their host *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) from three plant species, six times during the summer of 2013. We analyzed the effects of host abundance, plant species, and flowering state on parasitoid abundances. The abundances of three parasitoid species were significantly and positively affected by the abundance of *B. tabaci* on plants, regardless of plant species. In contrast, the abundance of the fourth species was not affected by host numbers, but rather by plant species identity as well as by flowering state: parasitoid numbers were lower on flowering plants than on non-flowering plants. Although previous field studies have shown correlations between parasitoid and host abundance, our research demonstrates additional, plant-related variables that can influence this relationship when hosts are

polyphagous. We also show that although having the same host, different parasitoid species respond differently to host- versus plant-related variables.

Keywords Aggregation · *Encarsia* · *Bemisia tabaci* · Density-dependence · Polyphagous hosts

Introduction

The abundance of hosts is an important limiting factor to parasitoid fitness. Beyond affecting parasitism rates in various ways (Walde and Murdoch 1988; Gunton and Pöyry 2015), host abundance also influences the distribution of their parasitoids among individual plants. In some cases, parasitoids were found to aggregate on plants with high host densities (Waage 1983; Hassell 2000; Bezemer and Mills 2001; Umbanhowar et al. 2003). This positive density dependence can result from the parasitoids' orientation toward host-infested plants, their reduced tendency to leave them, or from higher emergence of adults on heavily infested plants than on lightly infested ones (Sheehan and Shelton 1989). Although this response was documented for some parasitoids in the field, additional studies show that other factors can also determine parasitoid abundance. These may result in inverse density-dependent (Connor and Cargain 1994; Paull et al. 2014) or density-independent responses of parasitoid abundance to host availability (reviewed by Stiling 1987; Walde and Murdoch 1988; Heimpel and Casas 2008).

Parasitoids of polyphagous hosts seek them on a variety of plant species. Thus, they have to allocate their foraging effort across plant species, as well as among plant individuals within each species. Such parasitoids often favor specific plants species, regardless of how many hosts they

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harbor (Rabb and Bradley 1968; Vinson 1976). Some factors that affect parasitoid abundance on plants are abiotic, such as temperature, humidity, light intensity, and wind (Vinson 1976), and are related to the microenvironment of the plant (Bezemer and Mills 2001; Cronin and Haynes 2004; Kruidhof et al. 2015). Other factors are biotic and relate directly to plant traits. Plant blooming state, chemistry, and morphology are salient plant-related factors that influence habitat selection by parasitoids, as demonstrated by the following studies:

Blooming state affects parasitoid abundance because feeding on a sugar source, such as floral nectar, enhances survival and fecundity in many parasitoids (Lewis et al. 1998; Siekmann et al. 2001; Winkler et al. 2006). Plants in full bloom can therefore attract more parasitoids than non-flowering conspecifics (Wäckers 1994, 2004). Another factor, semiochemical profile, might influence parasitoid abundance because their habitat choices can be affected by chemical signals emitted as part of defense mechanisms by plants. For example, chemical signals produced by plants in response to herbivore attack may attract host-foraging parasitoids (Hare 2011; Mumm and Dicke 2010; McCormick et al. 2012; Mithöfer and Boland 2012). In addition, different plant species that vary in volatile composition often attract parasitoids differently, regardless of host abundance. This was demonstrated in the parasitoid *Cotesia kariyai* (Hymenoptera: Braconidae), which preferred maize to Japanese radish or kidney bean, even though all three plants were infested by identical numbers of hosts (Fujiwara et al. 2000). Finally, parasitoid abundance can also be affected by plant morphology, because it determines the efficiency of host-searching (Andow and Prokrym 1990). For example, parasitoids may prefer to seek hosts on plant species with smooth surfaces, even if infested by fewer hosts, than to forage on plants with rough surfaces (Vinson 1976; Inbar and Gerling 2008). Van Lenteren et al. (1976) showed that when the parasitoid *Encarsia formosa* searches for a host on a leaf, walking speed is reduced by leaf venation and high trichome densities.

While many studies investigated how parasitoid abundance is influenced by either host density or plant traits, the combined effect of both host abundance and plant characteristics on parasitoid distribution received much less research attention. In the present study, we asked whether parasitoids that attack a polyphagous host aggregate on individual plants with high host densities, and whether plant-related factors (plant species and flowering state) also account for the parasitoids' abundance on the plants under semi-field conditions. We hypothesized that parasitoids of polyphagous hosts are evolutionarily selected to choose foraging habitats that offer an optimal combination of host and plant resources. Hence we predicted that parasitoid abundances will be affected by both host density and plant traits.

Materials and methods

Study species

We focused on the fine-scale spatial distribution of parasitoid species of the genus *Encarsia* (Hymenoptera: Aphelinidae) that parasitize the same host, *Bemisia tabaci* (Hemiptera: Aleyrodidae), on three plant species. *B. tabaci* lives mainly on herbaceous plants and feeds on their phloem. It is highly polyphagous and is a major pest of various agricultural crops (De Barro et al. 2011). Consequently, *Encarsia* parasitoids of *B. tabaci* can locate their host on a variety of plant species. Research on *Encarsia* species shows that, in addition to ovipositing, wasps may also host-feed or feed on honeydew secreted by their host (Liu et al. 2015). Host feeding involves puncturing the host cuticle with the female's ovipositor followed by the consumption of its hemolymph fluids. In *Encarsia formosa* for example, host feeding results in the death of the host (Dai et al. 2014).

The three plant species used in our study are yarrow, *Achillea millefolium* L. (Asteraceae); celery, *Apium graveolens* L. (Apiaceae); and Syrian oregano, *Origanum syriacum* L. (Lamiaceae). These plants were previously tested as nectar sources for parasitoids in conservation biocontrol programs and are host plants for *B. tabaci*. Yarrow is often used in commercial beneficial insect habitat seed mixtures (Braman et al. 2002; Forehand et al. 2006) although some studies showed it to be under-visited in comparison to other plants (Colley and Luna 2000) or even to repel parasitoids (Wäckers 2004). Celery was investigated as a potential companion plant that repels some pests (Parker et al. 2013) and in commercially available beneficial insect habitats (Forehand et al. 2006). Syrian oregano was proven to be attractive to parasitoid wasps and its flowers provided accessible nectar that resulted in parasitoid weight gain (Wäckers 2004). Celery and Syrian oregano are native to the study area and yarrow is a foreign species often used as a decorative plant in private gardens.

Study area and sampling design

The study was performed in an experimental pomegranate orchard in the Hefer Valley, central Israel (32°22'48N, 34°55'58E). The four-hectare orchard consists of 44 rows of six-year-old pomegranate trees of the cultivar 'Wonderful.' The orchard hosted an experiment in biological control that explored the potential of enhancing the community of natural enemies by planting various non-crop plant species. We collected arthropods from 27 plant individuals divided equally between common yarrow, celery, and Syrian oregano. These individuals were planted along three rows (two ends and the middle row, nine plants

per row—see Fig. 1), in a randomized block design, in May 2013. The plants were fertilized and drip-irrigated throughout the season.

We sampled arthropods six times during a two-month period from July 17, 2013 to September 17, 2013, roughly at two-week intervals. The samples were collected before 10 am since temperatures are usually very high (>30 °C) during later hours in the summer and this can decrease *Encarsia* activity (Bayoumy et al. 2013). Each plant was sampled individually for 15 s using a Vortis Insect Suction Sampler (Burkard Manufacturing Co. Ltd, Rickmansworth, UK), and samples were preserved in 70% ethanol until classification. This method was previously shown to be effective for the determination of diversity and assemblage structure of arthropods in low-lying vegetation (Brook et al. 2008). Each plant was documented either as flowering or as non-flowering. Plants which had most of their flowers still in buds or those that comprised mostly withered flowers were considered as non-flowering.

Parasitoids from the genus *Encarsia* were classified to the species level. All *Encarsia* species sampled are reported in the literature to parasitize whiteflies. We therefore classified the suction-sampled whiteflies to the species level as well. Identification of parasitoid wasps and information about their host ranges were based on Hayat (1983), Rivnay and Gerling (1987), (Woolley 1997), Polaszek et al. (1992), Evans (2007), and Noyes (2003). Voucher specimens have been deposited in the National Collection of Insects, The Steinhardt Zoological Museum at Tel Aviv University, Israel.

Statistical analysis

We analyzed the effects of host abundance, plant species, and flowering state on parasitoid abundance for each *Encarsia* species separately, using data at the individual plant scale. For each species, we generated a linear mixed model

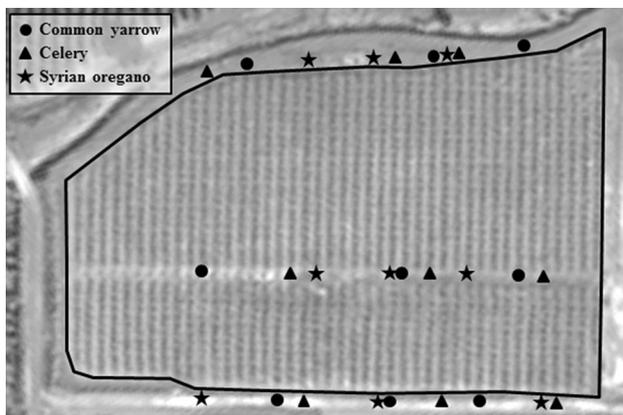


Fig. 1 Locations of plants sampled in the pomegranate orchard

with host abundance, plant species, and flowering state as fixed effects, and location (orchard row) and sample number (plant ID) as random intercept effects to account for the spatially nested structure of our data, as well as for its temporal structure (six sampling dates per plant). We first developed each model with interactions between host abundance and flowering state, and between host abundance and plant species identity, to test whether parasitoid abundance is driven by an interaction between host abundance and plant species. We could not test for a three-way interaction among all fixed effects because the model became rank deficient. Since we did not find significant interactions for any parasitoid species, we generated all models without interaction terms. Models were fit using the maximum likelihood criterion to facilitate the evaluation of the significance of fixed effects using Wald's type II Chi-square tests. We conducted all statistical analyses in R (R Core Team 2013) using the 'lme4' (Bates et al. 2014) and 'car' packages (Fox and Weisberg 2011). To check whether our models were affected by spatial autocorrelation in the data, we analyzed empirical variograms of the residuals of all of our models. We found no evidence for spatial autocorrelation.

Results

Parasitoids and hosts

We sampled and classified 149 individuals of five *Encarsia* species. Four of them, *E. inaron* (Walker) (only one individual collected from this species), *E. longifasciata* (Hayat), *E. lutea* (Masi), and *E. sophia* (Girault and Dodd) are found worldwide and can parasitize many species of Aleyrodidae including *B. tabaci*. *E. reticulata* (Rivnay) was only found once before and is known to parasitize only *B. tabaci* (Rivnay and Gerling 1987; Heraty et al. 2007). *E. lutea* and *E. sophia* are endoparasitoids and are heteronomous hyperparasitoids—females develop on homopterans as primary hosts, while males develop as hyperparasitoids of either their own species or related ones. *E. lutea* parasitizes the second to early fourth instar larvae of *B. tabaci* (Gerling and Foltyn 1987). *E. sophia* parasitizes all nymphal instars of *B. tabaci* except the late fourth instars (Yang et al. 2012). Both *E. lutea* and *E. sophia* perform host feeding. The biology of *E. longifasciata* and *E. reticulata* is unknown. Altogether, 1024 individuals of the host *B. tabaci* were sampled. Hosts colonized the plants freely and their numbers varied among individual plants. Host abundance generally increased throughout the sampling period and ranged from 76 to 294 individuals per sampling date. All of the sampled *Encarsia* species parasitize young stages of *B. tabaci*. Nevertheless,

because *B. tabaci* nymphs attach to the leaf surface, the vast majority of *B. tabaci* captured were adults. We considered all *B. tabaci* collected as potential hosts, assuming they are a good indicator to host abundance. We did not find any Diaspididae or other Aleyrodidae species apart from *B. tabaci* on the sampled plants.

Parasitoid dynamics throughout the sampling season

Encarsia numbers varied among individual plants. All *Encarsia* species collected were present in small numbers at the beginning of the sampling period (Fig. 2). Only *E. lutea* was present on the first collecting date (17 July). The other species were collected in higher numbers from the end of August until early September. However, the number of individuals of all species dropped on the final sampling date (17 September). The fact that parasitoid abundance increased over the first few samples indicates that they recolonized the plants between sampling sessions. *E. lutea* and *E. longifasciata* were collected in the highest numbers in early August and had another peak in abundance in early September. The largest numbers of *E. sophia* were found in mid-August. *E. reticulata* was found in small numbers overall, mostly in the middle of the sampling period. *E. inaron* was collected only once in the beginning of August and was therefore excluded from the statistical analysis.

Effects of host abundance, plant species, and flowering state on parasitoid abundance

The abundances of three out of four parasitoid species (*E. lutea*, *E. longifasciata*, and *E. sophia*) were significantly and positively affected by the abundance of *B. tabaci* on plants, regardless of plant species (effect sizes were $\beta = 0.079$, S.E. = 0.009, $\chi^2 = 66.4$, $p < 0.001$;

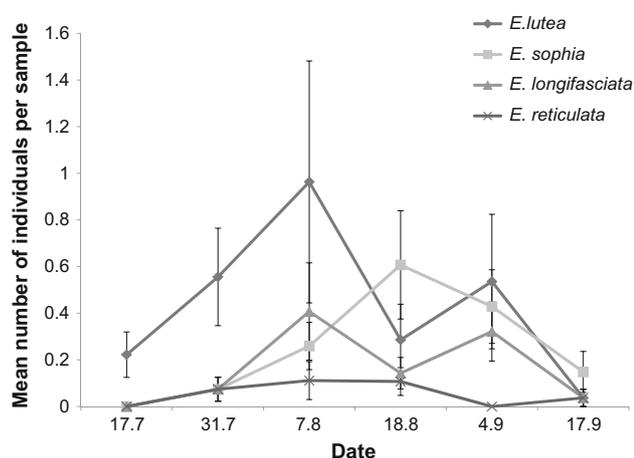


Fig. 2 Mean abundance of *Encarsia* species per plant throughout the sampling season. Error bars denote standard errors

$\beta = 0.019$, S.E. = 0.004, $\chi^2 = 18.2$, $p < 0.001$; and $\beta = 0.024$, S.E. = 0.005, $\chi^2 = 19.63$, $p < 0.001$, for the different *Encarsia* species, respectively) (Table 1). In contrast to the above species, the abundance of *E. reticulata* was not affected by host numbers, but rather by plant species identity ($\chi^2 = 7.92$, $p = 0.019$) as well as the flowering state ($\chi^2 = 4.05$, $p = 0.044$). The abundance of *E. reticulata* was significantly lower in celery plants compared to yarrow ($\beta = -0.217$, S.E. = 0.084, $\chi^2 = 6.56$, $p = 0.01$) and was significantly higher when plants were not in bloom ($\beta = 138$, S.E. = 0.069, $\chi^2 = 4.05$, $p = 0.044$).

Discussion

In this study we explored variables related to parasitoid abundance on plants. We found that host abundance, plant species, and plant flowering state can all affect parasitoid abundance, but that their effects differ among parasitoid species. Given that we expected that parasitoid abundances will be affected by both host density and plant traits, our finding that three species responded to host abundance while another species responded solely to plant species and its blooming state is surprising, especially since all of the parasitoids belong to the same genus, are morphologically similar, attack the same host, and were sampled in the same habitat.

Three of the four *Encarsia* species, *E. lutea*, *E. longifasciata*, and *E. sophia*, aggregated on plants highly infested with their host, *B. tabaci*. This density-dependent response can indicate that the wasps arrive in higher numbers to plants with high host abundance. An aggregated response on different plant species means that the wasps either orient to cues produced solely by their host, or can detect signals from different plants harboring their host. The exact mechanisms by which *Encarsia* species find their host is unknown, but Birkett et al. (2003) found that the congener *E. formosa* is attracted to plants that emit volatiles as a response to feeding by the parasitoid's host. The aggregation on plants with high host numbers may also be due to parasitoids staying longer on the infested plants, emerging on them in higher numbers or visiting them more frequently for host- or honeydew feeding.

Positive density-dependent responses of parasitoids were recorded in previous field studies. Our study differs from most of the previous experiments in that we did not control the number of hosts, but instead allowed them to colonize the plants freely (Waage 1983; Summy et al. 1985; Umbanhowar et al. 2003; but see Bezemer and Mills 2001; He and Wang 2014). The advantage of our method is that it represents the natural setting more closely. On the other hand, factors which we did not measure could have

Table 1 Results of the linear mixed models for the abundance of *Encarsia* species

<i>Encarsia</i> species	Explanatory variables		
	Host abundance	Flowering	Plant species
<i>E. lutea</i>	Positive ($p < 0.001$)	NS	NS
<i>E. longifasciata</i>	Positive ($p < 0.001$)	NS	NS
<i>E. sophia</i>	Positive ($p < 0.001$)	NS	NS
<i>E. reticulata</i>	NS	Negative ($p = 0.044$)	Affected ($p = 0.019$)

NS nonsignificant effect

influenced the abundance of both hosts and parasitoids. Differences in the plants' structure were not measured and could play a role in parasitoid foraging (Andow and Prokrym 1990). We assume that the differences between plants from the same species on each sampling date were minimal, since they were of the same age, had the same irrigation and fertilization regime, and were planted in the same soil. In addition, plant location, which could influence plant growth, was taken into account in the statistical analysis.

E. reticulata was the only species we sampled whose abundance was not influenced by host numbers. The abundance of other parasitoid species was found to be independent of host availability as well (Stiling 1987; Walde and Murdoch 1988). One of the possible reasons for *E. reticulata*'s distribution could be avoidance of patches where conspecifics or heterospecifics are present. Janssen et al. (1995) found that *Leptopilina heterotoma*, a parasitoid of *Drosophila* larvae, avoids host patches where *L. clavipes*, another parasitoid of the same host, is present. *E. reticulata* was also the only species whose abundance was influenced by plant species. It was more abundant on yarrow than on celery. It is possible that *E. reticulata* is less attracted to celery or tends to avoid it due to the presence of unattractive volatiles or sub-optimal surface structure. *E. reticulata* was also affected by flowering state—it was found in smaller numbers on plants in full bloom than on plants that had no flowers. It is possible that this is due to interference by other *Encarsia* species or by other parasitic or predatory arthropods. The numbers of *E. lutea*, *E. longifasciata*, and *E. sophia* were not affected by the flowering state of the plants. It is possible that these species feed on nectar sources from other plants or, as was found for *E. formosa*, feed on the honeydew that their host secretes.

Our study focused on *Encarsia*'s aggregative response rather than on its functional response. Consequently, we did not examine the parasitism rate of *B. tabaci* by *Encarsia* species, and therefore, we do not know whether the numbers of parasitoids on the plants correlate with parasitism rates. A recent meta-analysis found that parasitism is usually positively density dependent when the host was from the Homoptera suborder (Gunton and Pöyry 2015).

On the contrary, Simmons (2000) found that *B. tabaci*'s parasitoid *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) aggregated on leaves with high host densities, but that parasitism was density independent, due to egg limitation or interference.

This study demonstrates the interplay among variables that can affect parasitoid abundance on plants. We show that the presence and abundance of parasitoids on a given plant individual can often be explained by host abundance, but that the plant's flowering state and identity can also be important. Generally, the abundances of different parasitoid species are influenced by different combinations of these factors. This is probably due to subtle differences among closely related parasitoid species in host range, non-host diet, phenology, and competitive ability. These species-specific responses to host- vs. plant cues contribute to the wide range of parasitoid aggregation patterns reported in the literature.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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