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Trait-based characterisation of parasitoid wasp communities in natural and agricultural areas

Miriam Kishinevsky[1] | Tamar Keasar[2]

[1]Department of Evolutionary and Environmental Biology, University of Haifa, Haifa, Israel

[2]Department of Biology and the Environment, University of Haifa – Oranim, Tivon, Israel

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

Present address
Miriam Kishinevsky, Department of Integrative Biology, University of Wisconsin, Madison, Wisconsin, 53706, United States

Abstract

1. Life-history traits are increasingly used to understand how arthropod communities assemble and function under diverse conditions, for example why some species are better adapted to agricultural intensification than others. We aimed to understand which traits characterise parasitoid wasps under agricultural disturbances. To this end, we studied parasitoid communities from pomegranate orchards and nearby natural habitats in Israel.

2. Ten sites along a climate gradient were sampled thrice along one fruit-growing season. We compiled information on life-history traits associated with development, adult diet and host taxa, for 27 well-represented parasitoid species. We tested for relationships between the parasitoids' abundances, functional traits and environmental conditions, using RLQ and fourth-corner analyses.

3. Life-history traits were highly related to environmental variables. Koinobionts (wasps whose parasitized hosts feed and grow), and parasitoids of aphids and whiteflies, were more common, and sugar-feeding was less common, in orchards than in natural habitats. Parasitism of larval hosts correlated with aridity, while egg parasitism increased with herbaceous vegetation cover.

4. Host composition and koinobiosis shape parasitoid communities in the orchards. Koinobiosis is often associated with life-history traits such as small eggs, short lifespan, early egg maturation and high fecundity, which may be adaptive in the frequently disturbed orchard habitats. Further, dense vegetation conditions seem to favour egg parasitism (perhaps because of reduced risks of egg desication), while larval parasitism is more common in arid seasons and sites. These findings provide initial insights regarding the effects of land use and climate on the functional characteristics of parasitoid communities.

KEYWORDS
agroecology, functional traits, koinobiosis, parasitoid community composition, phenology, pomegranate

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INTRODUCTION

Agriculture, the most widespread form of land use, takes up more than one-third of the global landmass and is increasingly impacting natural ecosystems (Wanger et al., 2020). The abundance, species richness and functional diversity of many plants, animals and microbes are lower on farmlands than in natural habitats, especially in monocultures with high inputs of agrochemicals (Lichtenberg et al., 2017). Specifically, the abundance and diversity of beneficial insects (pollinators and biological control agents) decline with increasing proportions of agricultural habitat in the landscape (Chaplin-Kramer et al., 2011; Kennedy et al., 2013). Intensively managed croplands are ploughed, fertilised, sprayed, trimmed and harvested – all of which are potential sources of disturbance to resident insects. They are also often poor in essential resources for beneficial insects, such as floral nectar (Kishinevsky & Keasar, 2021) and nesting substrates (Williams et al., 2010). Such stressors constitute ecological filters, which allow only a subset of species to establish and thrive in the agricultural plots. Consequently, insect communities often differ considerably between croplands and adjacent natural areas (Derocles et al., 2014; Shapira et al., 2018).

Functional traits provide insights into species' adaptations to their environments. They help to understand how ecological communities assemble and work (Moretti et al., 2017), and to identify which communities are more at-risk facing land-use intensification. Initial studies on some insect communities have generated insights into traits that allow insects to cope with agricultural disturbances (Börschig et al., 2013; Perović et al., 2018; Vandewalle et al., 2010). Multivoltine insect species with high fecundity and long lifespans are less prone to extinction in agricultural plots than low-fecund, univoltine and short-lived species, presumably because they can better recover from disturbances. Likewise, species with generalist diets (Rand & Tscharntke, 2007) and high mobility (Börschig et al., 2013) are more likely to persist in intensive agroecosystems than low-dispersing specialists, as they are able to use alternative food sources and habitats when the fields are disturbed. Finally, large-bodied insects are often more sensitive to in-field agricultural intensification than small-bodied insects (Birkhofer et al., 2017, but see Gámez-Virués et al., 2015 for conflicting results). This may result from food shortages in the agricultural habitats that limit growth (Oliveira et al., 2016), or from selection for small, quickly-developing individuals in the often-disturbed farm habitats (Neff et al., 2020). These patterns, or subsets of them, were confirmed in studies that compared species composition and functional traits along gradients of agricultural intensification. The taxa tested so far include pollinators (Rader et al., 2014), ground beetles (Hanson et al., 2016), spiders (Hanson et al., 2017), herbivorous hemipterans (Neff et al., 2020) and other insect pests (Tamburini et al., 2020). Here, for the first time, we extend the functional trait perspective to communities of parasitoid wasps.

Parasitoid wasps are important secondary consumers in arthropod communities and key natural enemies of agricultural pests. They lay their eggs in or on the body of their arthropod hosts, which are consumed by the wasps' developing larvae. This makes them effective control agents of many arthropod crop pests (Heimpel & Mills, 2017). Numerous studies from different parts of the world describe parasitoid abundance and activity from diverse agricultural crops under different management practices (Bianchi et al., 2006). These descriptions are mostly focused on pest control rates (e.g., Derocles et al., 2014; Feng et al., 2017), with little attention paid to functional traits as adaptations to specific environments. Consequently, little is known about the suites of traits that shape assemblages of parasitoids in agroecosystems (Perović et al., 2018). Namely, which traits allow some parasitoids to thrive in croplands. This knowledge gap limits our ability to understand community function and to guarantee the successful establishment of natural enemies in biological control interventions.

Agricultural disturbances affect insect communities in the short-term ecological timescale as well as in long-term evolutionary time. At the ecological time-scale, it is important to consider the short-term effects of specific disturbances on the abundance, spatial distribution and fitness of insects. At the evolutionary level, on which we focus here, life-history traits are hypothesized to be shaped by natural selection as adaptations to local conditions. Species that are adapted to the frequent and diverse disturbances caused by farming are thus expected to dominate agricultural plots, whereas species that are sensitive to disturbance are predicted to inhabit natural habitats.

Parasitoids are diverse and ubiquitous in Israel's agroecosystems (Segoli et al., 2020; Shapira et al., 2018). In previous studies of Israeli wine-producing vineyards, parasitoid abundances were higher on non-crop herbaceous vegetation than on the vines, while their relative abundance in agricultural versus neighbouring natural habitats varied between sites and seasons. Species composition differed significantly between the two habitats (Segoli et al., 2020; Shapira et al., 2018). Following applications of a pesticide that targets Lepidoptera, the total abundance and species richness of parasitoids declined transiently. The community composition shifted toward a lower representation of common species that parasitize lepidopterans (Schindler et al., 2022). Sugar feeding by adult parasitoids greatly improves longevity and fecundity in most species, as compared with unfed individuals (Thompson, 1999). Potential sugar sources include floral nectar, extrafloral nectar, honey-dew secreted by sap-feeding insects, and even rotting fruit. We do not know the source of the sugar in the natural and agricultural areas of this system. We do know that the proportion of sugar-fed wasps is lower within vineyards than in neighbouring natural habitats and that it declines from spring to winter in both habitats (Kishinevsky & Keasar, 2021). Similar low levels of sugar feeding occurred inside pomegranate orchards (Kishinevsky et al., 2018), the focus of the present study, pointing to sugar as a limiting resource.

We repeatedly sampled wasps from 10 pomegranate-growing sites and adjacent semi-natural habitats. The study sites differed in climate and agronomic conditions. We documented 11 environmental variables, related to climate and land-use, per site. We also recorded six functional traits that characterise the life-history strategy of each focal parasitoid species. We tested for links between environmental and habitat conditions, the parasitoids' traits, and the variability in community composition.

Host densities are expected to be higher in croplands than in natural habitats (Shapira et al., 2018) because the agricultural crop offers concentrated plant resources for herbivores. Owing to farming disturbances, parasitoid mortality is expected to be higher in the orchards than in natural areas, whereas sugar availability is predicted to be lower in the orchards. Hence, the parasitoids' levels of investment in reproduction versus longevity may affect their habitat preferences. Direct reproductive measures (such as egg load or size) are not available for most of the species in our study. Instead, we classified our study species as either idiobionts (parasitoids that stop host development at parasitism) or koinbionts (allowing host development to continue). Koinobiosis is a key developmental feature in parasitoids, which correlates with short adult life-spans, high fecundity, and early egg maturation (Mayhew & Blackburn, 1999), that is, a life-history strategy that prioritises fecundity over longevity.

We hypothesized that frequent disturbances in the agricultural plots would select for the following traits at an evolutionary time-scale: (1) A higher investment in reproduction, at the expense of adult longevity, manifested as increased koinobiosis; (2) lower reliance on sugar feeding than in the natural habitat, since sugar limitation is more severe inside the crop plot; (3) development on concealed hosts, since this can allow parasitoids to evade some agricultural disturbances and (4) lower community-weighted body size and more egg parasitism in the agricultural habitat since egg parasitoids develop faster, and into smaller adults, than larval parasitoids (Traynor & Mayhew, 2005). This hypothesis is based on previous evidence that small-bodied insects survive agricultural disturbances better than larger species (Birkhofer et al., 2017).

In comparisons across arthropod taxa, groups with broad diets (such as spiders and polyphagous butterflies) increased in abundance with the intensity of agricultural management (Gámez-Virués et al., 2015; Perović et al., 2018). Since the host specificity of our parasitoids is not sufficiently known, we were not able to test whether host range breadth correlates with habitat in our dataset. We did, however, tabulate the broad taxonomic group of hosts associated with each parasitoid species, based on the published information. That is, we treated a parasitoid's host association as one of its traits. This allowed us to test for correlations between the parasitoids' feeding guilds and the environmental variables.

MATERIALS AND METHODS

Study area and sampling design

Ten locations across a 250-km climate gradient in Israel, along which the mean annual precipitation ranges from 91 to 611 mm, were chosen. A commercial non-organic pomegranate orchard (cv 'Wonderful') was situated at each sampling site. All orchards were treated with herbicides and insecticides according to the guidance of an extension specialist, and each bordered a natural, untreated area on at least one of its sides. Arthropods were suction-sampled from herbaceous vegetation in these natural areas. Six samples were collected per sampling
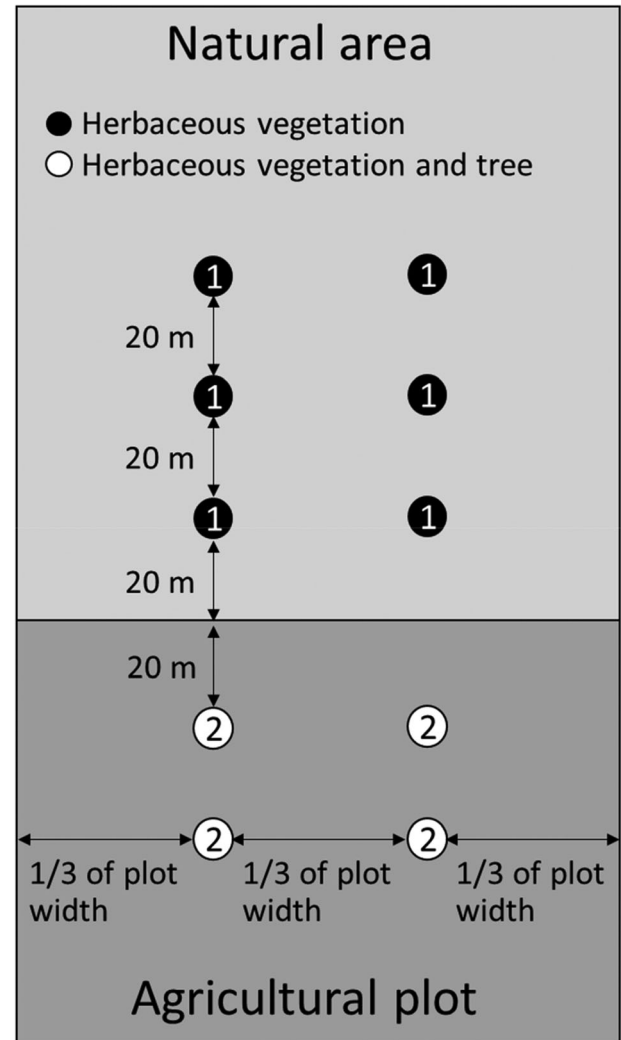

FIGURE 1 The sampling design in each study site. Light-grey and dark-grey areas denote agricultural and natural habitats. The sampling locations along the two transects are indicated by circles. The number of samples collected at each point (either one from the herbs, or one from the herbs and one from the trees) are noted inside the circles

site and date, along two transects in the herbaceous natural vegetation at 20, 40 and 60 meters from the orchards' margin into the natural habitat. Eight additional suction samples were collected inside the orchards on each site and date, along the two transects. Four of these samples were collected from the middle of each orchard and four were collected 20 meters away from the orchard's border with the neighbouring natural area. In each of these sampling points, a sample was taken from the pomegranate trees and another was taken from the herbaceous vegetation (if present) directly beneath them. This was done to distinguish between the effects of habitat (orchard vs. natural) and of plant life-form (tree vs. herb) on parasitoid life-history traits. Because of the proximity between the herbaceous vegetation and the pomegranate trees within the orchards, some migration between them cannot be ruled out. Nevertheless, we found significant differences in the parasitoid community composition between the two habitats in a previous study (Kishinevsky et al., 2018).

Figure 1 illustrates the sampling locations. This design generated 140 samples per sampling date, collected from the natural area (60 samples) and the orchards (80 samples). All sites were sampled three times (in June, August and October) during the summer of 2015, resulting in 420 samples. Summer is the fruit growing season of pomegranate and many other fruit crops in Israel, and both pests and natural enemies are active during this time. Samples were collected using a Vortis Insect Suction Sampler (Burkard Manufacturing Co. Ltd, Rickmansworth, UK) and stored in 75% ethanol at −35°C until classification. From previous work in the same study sites, we learned that large numbers of arthropods, including small hymenopterans, are collected from most habitats by suctioning for 15 s. We also found that pomegranate trees yield about a quarter of the number of arthropods per suction sample compared to herbaceous vegetation. We, therefore, sampled for 60 s from the pomegranate trees. The longer sampling durations in the tree canopies do not affect our analyses and conclusions, since we do not compare species richness or abundances between habitats. Parasitoids were identified as species when possible. The remaining specimens were identified to family or genus, then sorted into morpho-species. Parasitoids were identified based on Doutt and Viggiani (1968); Hayat (1983); Goulet and Huber (1993); Chiappini et al. (1996); Noyes (2003); Pinto (2006); Huber et al. (2009); and Aishan et al. (2015).

Environmental variables

We recorded the month and the habitat in which each sample was collected: semi-natural areas neighbouring the orchards ('Nature'), herbaceous vegetation within the orchards ('Agri'), or the pomegranate trees ('Pome'). The abiotic conditions documented for each site included mean monthly temperature, monthly temperature amplitude ('Delta temperature') and annual rainfall. Temperature data for each location were compiled from the Israel Meteorological Service database (www.ims.gov.il/IMSEng/CLIMATE). Daily data were averaged over the month before each sampling date for each orchard. Temperature conditions affect parasitoid populations directly by influencing developmental time and dispersal abilities, and indirectly by affecting their hosts and host plants (Abram et al., 2017; Hance et al., 2007). The long-term mean annual precipitation per orchard was also included as an important climatic driver of species distributions (Kadmon & Danin, 1999; Pe'er et al., 2011). Israel is characterised by steep north–south and west–east climatic gradients, with aridity and seasonal temperature variation increasing toward the south and east. We therefore also listed each site's latitude and longitude as additional climate proxies.

We evaluated the effects of land-use and agricultural activities by incorporating the following variables: orchard area; percent of herbaceous vegetation cover and non-crop plant species richness within the orchard; and Normalised Difference Vegetation Index (NDVI, an index of live green vegetation cover, derived from remote sensing) in the surrounding landscape. Table S1 summarises the environmental variables recorded.

Insect traits

We obtained the following traits from the literature: (1) the host taxon of each parasitoid species; (2) whether hosts are typically exposed on the surface of plant leaves or concealed within plant tissues as eggs or nymphs/larvae; (3) whether the parasitoids attack their hosts at the egg stage or as nymphs/larvae; (4) whether parasitoids are ecto- (external), endo- (internal) or ecto-endo (first external, later internal) parasites and (5) whether their host stops developing after parasitism (idiobiosis) or not (koinobiosis). We also tabulated (6) the proportion of sugar-fed individuals in each of the 27 parasitoid species, which we recorded in previous community-level surveys in natural habitats (Kishinevsky et al., 2018; Kishinevsky & Keasar, 2021). We used these proportions as a measure of each species' sugar-feeding needs. Probably due to its high correlation to other life-history traits (such as host stage) body size was not associated with either of the habitats or the climate-correlated environmental variables in preliminary analyses. It was therefore not included as an explanatory variable in our final statistical models. We were able to obtain information on all six traits for twenty-seven species that were also common (≥20 individuals in all samples combined) and well-identified (to genus or species). These parasitoids, which are all primary and solitary, were included in the trait-environment analyses. The species traits are listed in Table S3.

Data pre-processing and descriptive statistics

Parasitoid counts for each site-month-habitat combination were averaged, resulting in 90 samples (10 sites × 3 habitats × 3 months). We calculated the community-weighted mean (CWM) value of each trait in each sample and averaged the CWM trait values for the 'Nature', 'Agri' and 'Pome' habitats. These provided descriptive statistics that allowed us to detect differences in community characteristics between the three habitats. In these calculations, body size and sugar-feeding frequency are considered continuous variables. Idio/koinobiosis, host exposure/concealment and egg/larval parasitism were treated as binary variables. Host type, a categorical variable with eight levels (Aleyrodidae, Aphididae, Auchenorrhyncha, Brachycera and Lepidoptera, Cecidomyiidae, Heteroptera, Lepidoptera, Pseudococcidae), was converted into eight dummy variables. Similarly, ecto/endo/ecto-endo parasitism was converted into three dummy variables. Phylogenetic distance between the tested parasitoids is likely to influence the similarity in their functional traits. However, phylogenies for our study species are not yet complete enough to allow formal phylogenetically-corrected analyses. Instead, to informally explore the effects of shared ancestries, we ran an additional set of analyses in which we added each species' family as a trait variable. This trait was not significantly correlated with habitat or climate (results not shown).

Trait-environment analyses

We used the combined RLQ and fourth-corner methods to analyse the links between the parasitoids' traits and the environmental conditions in the 'Nature', 'Agri' and 'Pome' habitats. Both methods

require the construction of three data tables: Table R provides data of environmental variables by sample sites, Table Q contains traits by species information, and Table L reports the abundances of species in each of the sampling sites. These data form the input for constructing a fourth table, which describes the intensity of the links between the species traits and the environmental variables. In RLQ, the fourth table is used to summarise the main structures in the data along orthogonal axes and provides a global measure of the association between environmental variables and traits (Dray et al., 2014). It allows for identifying trait syndromes of species sharing similar traits and reacting similarly to different environments, as demonstrated for arthropod communities in grasslands (Gámez-Virués et al., 2015; Neff et al., 2020). In the fourth-corner analysis, the table is used to evaluate the multiple bivariate correlations between traits and environmental variables, accounting for biases generated by highly correlated traits. By combining the two methods, one can test the global significance of the trait–environment relationships using multivariate statistics, and also explore how individual functional traits change with environmental conditions (Méndez-Toribio et al., 2020).

Table R contained 11 environmental variables (Table S1) for each of the 90 samples, Table L contained abundance data for each of the 27 species in each of the 90 samples (Table S2), and Table Q listed six traits for each of the 27 species (Table S3). For the initial ordination steps of the RLQ analysis, we used correspondence analysis on the L Table. Since Tables R and Q contained both quantitative and categorical variables, we used the Hill-Smith method to produce their ordinations. We subsequently performed the RLQ analysis and verified that it captured much of the variance of the simple ordinations (0.85 of the variation was preserved for environmental variables, 0.78 for trait variables). We tested for the global significance of the trait–environment relationships. We also calculated the bivariate correlations between traits and environmental variables, using the Benjamini–Hochberg false discovery rate method to adjust p-values for multiple comparisons. The significance of the correlation tests was determined using permutation tests with 9999 permutations.

All statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020). We used the packages 'FD' (Laliberté & Legendre, 2010) and 'ade4' (Dray & Dufour, 2007) to calculate CWMs and to run the RLQ and fourth-corner analyses. The packages 'ggplot2' (Wickham, 2016) and 'ggrepel' (Slowikowski, 2018) were used to visualise the outputs.

RESULTS

The parasitoid dataset

Our dataset includes 2828 parasitoids of 27 identified species that belong to 8 families (Aphelinidae, Bethylidae, Encyrtidae, Eulophidae, Mymaridae, Platygastridae, Scelionidae, Trichogrammatidae). The most common species were *Telenomus* sp. 4 (10.43% of all specimens) and *Neochrysocharis formosus* (8.08%, Table S2). This dataset comprises 67% of all parasitoids in the suction samples. None of the

species were found exclusively in the natural habitat or in the agricultural habitat.

Trait-environment associations

Table 1 summarises the community-weighted mean values for each of the traits in the three habitats. The RLQ randomization test indicated highly significant associations between species abundances and environmental conditions ($p = 0.001$), as well as between species abundances and species traits ($p = 0.001$). Accordingly, the null hypothesis of no association between environmental conditions and parasitoid traits is rejected (fourth-corner test, $p < 0.0001$). The first RLQ axis explained 63.2% of the data variance and the second axis explained 20.8%. In other words, the parasitoids' life-history traits and environmental conditions account for 84% of the variation in their community composition. Trait and environmental variables associated with the first axis are more important than those associated with the second axis.

Positive values on the first axis (which captures most of the abundance-based variation in parasitoid traits) are associated with late summer (the most arid season) and with more eastern (arid) sites. Negative values are related to the high cover of herbaceous plants and high plant species richness. Thus, the first axis describes a climate and vegetation gradient, ranging from hot and dry to mesic, vegetation-rich, sites and seasons (Figure 2a, Table 2a). Parasitism on whiteflies (Aleyrodidae), ectoparasitism, koinobiosis and development on larval hosts were associated with positive values on the first axis (i.e., with arid conditions). Parasitism on planthoppers and leafhoppers (Auchenorrhyncha), endoparasitism, idiobiosis and egg parasitism are associated with negative values, that is with mesic conditions (Figure 2b, Table 2b).

The second axis is mainly associated with land use: positive values correlate with the agricultural ground cover habitat ('Agri'), while negative values correlate with the natural habitat ('Nature') (Figure 2a, Table 2a). Positive values on the second axis also correlate with endoparasitism, koinobiont development and exposed hosts. Negative values, on the other hand, correlate with parasitism on Lepidoptera and Brachycera, ectoparasitism and idiobiosis (Figures 2b, 3). The pomegranate tree habitat ('Pome'), while not significantly correlated with the two RLQ axes (Table 2a), is associated with aphid parasitism and with koinobiosis (Table 1, Figure 2a,b).

In line with our first two hypotheses, idiobiosis and reliance on sugar feeding were significantly associated with the natural habitat, while parasitoids from orchards tended to be koinobionts and to sugar-feed to a lesser extent. Contrary to our hypotheses 3–4, host exposure and the host stage attack did not associate with any of the habitats (Figures 2a,b and 3).

The parasitoid species formed three distinct clusters in the RLQ plot, based on their traits and environmental ranges (Figure 2c). One cluster, associated with the orchard habitat, includes six koinobiont species: three species of *Encarsia*, *Eretmocerus mundus*, *Anagyrus* sp. and *Aphelinus* sp. A second group contains 16 species linked to

TABLE 1 Community-weighted mean values of the parasitoid traits, averaged by habitat. Means ± SE of all samples from each habitat are reported

Trait	Habitat		
	Natural	Herbs in orchard	Pomegranate trees in orchard
Endoparasitism	0.87 ± 0.05	0.77 ± 0.06	0.87 ± 0.04
Ectoparasitism	0.13 ± 0.05	0.11 ± 0.04	0.05 ± 0.04
Koinobiosis	0.08 ± 0.02	0.33 ± 0.07	0.40 ± 0.07
Egg parasitism	0.71 ± 0.06	0.51 ± 0.07	0.47 ± 0.07
Sugar feeding	0.54 ± 0.01	0.42 ± 0.02	0.47 ± 0.03
Host exposure	0.43 ± 0.05	0.66 ± 0.06	0.79 ± 0.06
Host: Aleyrodidae (whiteflies)	0.03 ± 0.01	0.28 ± 0.07	0.34 ± 0.07
Host: Aphididae (aphid)	0.01 ± 0.01	0.03 ± 0.02	0.05 ± 0.03
Host: Auchenorrhyncha (leafhoppers & planthoppers)	0.31 ± 0.05	0.18 ± 0.05	0.08 ± 0.03
Host: Cecidomyiidae (gall midges)	0.02 ± 0.01	<0.01	<0.01
Host: Heteroptera (bugs)	0.02 ± 0.01	0.02 ± 0.01	<0.01
Host: Lepidoptera/ Diptera (Leafminers)	0.22 ± 0.07	0.06 ± 0.02	0.12 ± 0.06
Host: Lepidoptera (butterflies and moths)	0.05 ± 0.01	0.30 ± 0.06	0.07 ± 0.03
Host: Lepidoptera/Heteroptera (moths or bugs)	0.31 ± 0.05	0.12 ± 0.03	0.32 ± 0.07
Host: Pseudococcidae (mealybugs)	0.01 ± 0.01	0.02 ± 0.01	0.01 ± 0.01

Note: $n = 30$ (10 orchards × 3 months) samples from each habitat. Mean values for ecto-endoparasitism are not listed, because only one species in the dataset belongs to this category. When calculating community-weighted means, the sugar-feeding frequency was considered a continuous variable. The remaining traits were treated as binary variables. For these variables, the tabulated values indicate the proportion of species possessing a trait, weighed by their relative abundance in the parasitoid community.

high vegetation cover, and with a stronger association to the natural habitat than to the orchards. All of them are egg parasitoids, and all except one species are idiobionts. The third group, comprising two *Zagrammosoma* species, are late-season idiobionts and larval parasitoids of leafminers associated with the natural habitat. Two additional species (*Bethylus* sp. and *Neochrysocharis formosus*) did not cluster with any of the above groups.

DISCUSSION

Our analyses confirm that parasitoid communities in pomegranate orchards differ in life-history traits from their neighbouring communities in semi-natural habitats. We expected that ecological filtering within the orchards would select for traits that are advantageous under frequent disturbances. The high prevalence of koinobiosis in the orchard community is consistent with this prediction. Phylogenetically-controlled comparative studies of hundreds of parasitoid species revealed that koinobionts have smaller eggs, shorter adult life-spans, earlier egg maturation, higher oviposition rates and higher lifetime fecundity than idiobionts (Jervis & Ferns, 2011; Mayhew & Blackburn, 1999). This suite of traits combines rapid reproduction with low adult survival and is considered adaptive when hosts are abundant and conditions are unstable (Godfray, 1994; Mayhew, 2016). High host densities and unstable conditions often occur in agricultural habitats, thus the abundance of koinobionts in the orchards is in line with our first hypothesis. Indeed, intra-specific

comparisons in the parasitoids *Venturia canescens* and *Anagrus daanei* showed higher resource allocation to reproduction in human-disturbed habitats than in natural areas (Pelosse et al., 2007; Segoli & Rosenheim, 2013). A complementary interpretation is that developing parasitoids may experience more intra-guild predation, caused by arthropod predators feeding on their hosts, in natural habitats than in the orchards. This may favour idiobiosis in the natural habitat since idiobionts develop more quickly than koinobionts and hence faceless incidental predation as immatures. We note that the natural and the orchard habitats differ in additional variables, which may also contribute to the higher frequency of koinobiosis in the orchards. Experiments that manipulate each factor at a time are needed to tease apart their effects.

We also found support for our second hypothesis that sugar feeding would be less common in the orchard communities than in natural ones. Using data from previous studies on species-wise sugar feeding frequencies in natural areas, we estimated the community-level dependence on sugar feeding in our samples. Since sugar limitation is lower in the natural habitat than within the orchards, we consider sugar-feeding frequencies in natural habitats as better indicators of the species-wise requirement for sugar than frequencies of sugar feeding recorded in croplands. Orchard communities had lower sugar-feeding scores than parasitoid communities in the natural habitat. This could result from the lower availability of sugar sources within the orchard, which filters out species that highly depend on sugar feeding. Alternatively, if adult parasitoids indeed live longer in their natural habitats, they may simply have a longer time window
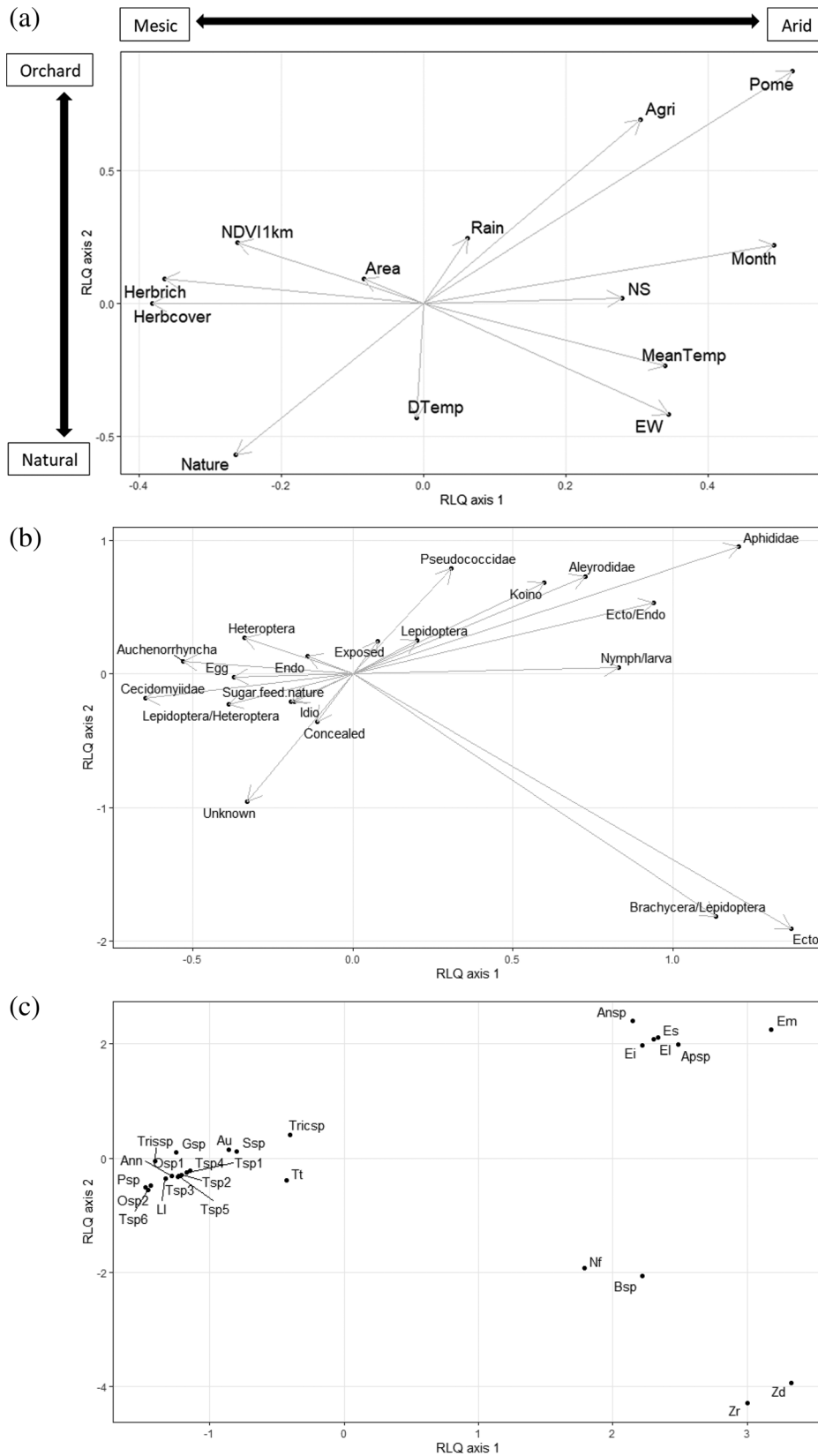
FIGURE 2 The ordination of (a) environmental variables, (b) traits and (c) parasitoid species on the RLQ plot. The length of the arrows indicates the strength of the effect of each environmental variable (Figure 2a) or life-history trait (Figure 2b) on community composition. Species names are abbreviated for graphical clarity. Full species names are provided in Table S3, and the variables' acronyms are explained in Table S4. The interpretations of the main environmental gradients correlated with the ordination axes are plotted as thick arrows

TABLE 2 Associations between the tested environmental variables (a) and the parasitoid traits (b) with the first and second axes of the RLQ plot

(a)

Environmental variable	First RLQ axis	Second RLQ axis
Month	Sig. positive	NS
Agricultural habitat	NS	Sig. positive
Natural habitat	NS	Sig. negative
Pomegranate habitat	NS	NS
Annual rainfall	NS	NS
Orchard area	NS	NS
Longitude	Sig. positive	NS
Latitude	NS	NS
Delta temperature	NS	NS
Mean temperature	Sig. positive	NS
Wild plant coverage	Sig. negative	NS
Plant species richness	Sig. negative	NS
NDVI 1-km radius	NS	NS

(b)

Parasitoid trait	First RLQ axis	Second RLQ axis
Host: Aleyrodidae	NS	NS
Host: Aphididae	NS	NS
Host: Auchenorrhyncha	Sig. negative	NS
Host: Brachycera and Lepidoptera	NS	Sig. negative
Host: Cecidomyidae	NS	NS
Host: Heteroptera	NS	NS
Host: Lepidoptera	NS	NS
Host: Lepidoptera or Heteroptera	NS	NS
Host: Pseudococcidae	NS	NS
Ectoparasitoid	Sig. positive	Sig. negative
Endoparasitoid	Sig. negative	Sig. positive
Idiobiont	Sig. negative	Sig. negative
Koinobiont	Sig. positive	Sig. positive
Egg parasitoid	Sig. negative	NS
Larval/nymphal parasitoid	Sig. positive	NS
Hosts: concealed	NS	NS
Hosts: exposed	NS	NS
Host concealment: Unknown	NS	NS
Sugar feeding frequency in natural habitat	NS	NS

Note: Statistically significant correlations ($p < 0.05$) are indicated as 'Sig. positive' or 'Sig. negative'. NS indicates the non-significant associations.

available for sugar feeding than the orchard parasitoids. In agreement with our findings, planting of nectar-rich plants in crop plots were found to change the species composition (Miall et al., 2020) and within-plot distribution (Kishinevsky et al., 2017) of resident parasitoid communities, possibly by attracting nectar-dependent species.

While these findings support our first and second hypotheses, two additional life-history traits – host exposure and host stage attack (hypotheses 3–4) – did not show the predicted trends. We predicted the agricultural areas to harbour more species, which attack concealed hosts and that develop in their host's egg stage (and hence tend to be small). These traits did not associate significantly with either the natural or the agricultural habitats. Interestingly, however, the host stage attack was strongly linked to climate-correlated environmental variables. Namely, egg parasitism dominated vegetation-rich sites, while larval parasitoids occurred in eastern (inland and dry) sites, during late summer (the driest season, as it follows several months with no rainfall). This link occurs along the first axis of the RLQ co-inertia analysis, thus it explains more of the variation in parasitoid community composition than agricultural/natural habitat. Possibly, herbivore egg mortality increases in arid sites and seasons due to desication. This may select for higher larval parasitism under arid conditions.

Some previous studies found that idiobiont parasitoids have broader host ranges than koinobionts (Mayhew, 2016), and that agricultural habitats favour insects with generalised diets (Rand & Tscharntke, 2007). Therefore, idiobiosis could be expected to dominate agricultural habitats, yet our dataset showed the opposite trend. This could be related to our choice of pomegranate, a perennial crop, as our study system. Since crop type remains constant across the seasons in our system, it is likely to have a stable community of herbivores, which specialised parasitoids are able to exploit. This hypothesis calls for experimental testing of the host ranges of the parasitoids in our communities, best accomplished using genetic tools (Derocles et al., 2014).

We did not formulate a specific hypothesis regarding the parasitoids' hosts in agricultural versus natural habitats. Nevertheless, we found that host type correlated with the distribution of parasitoids between the two habitats. The orchard-dwelling parasitoid community was rich in species that attack aphids and whiteflies, perhaps simply because aphids and whiteflies dominated the orchard habitat. These associations were independent of the parasitoids' life-history traits, even though members of a parasitoid guild sometime share common phylogenies and life-histories. This suggests that the correspondence between life-history traits and habitat does not simply reflect convergent adaptations of parasitoid species to the broad host taxa occupying these habitats. In agreement with our findings, a molecular analysis of an aphid-parasitoid food web found that the species composition of both hosts and their associated parasitoids differed substantially between crop fields and their semi-natural margins (Derocles et al., 2014).

Life-history traits within ecological communities can be influenced by regional environmental conditions, as well as by biotic interactions (such as interspecific competition) within the community. Differences in trait values between communities may arise from ecological filtering and/or phenotypic plasticity. Both mechanisms can
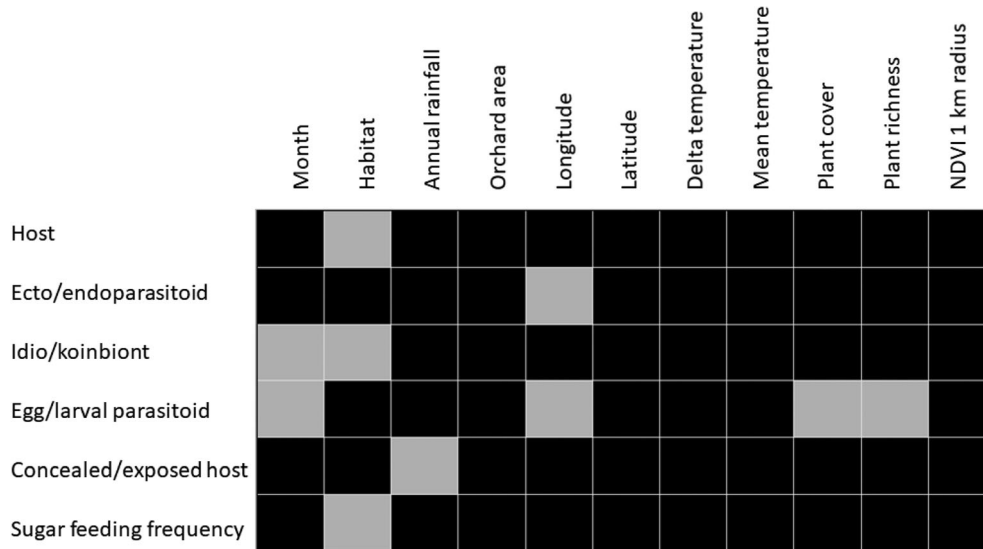
FIGURE 3 Summary of bivariate tests between parasitoid traits (rows) and environmental variables (columns). Statistically significant correlations at $p < 0.05$ are marked in grey

generate within-species differences in trait values across ecological communities (Raine et al., 2018; Segoli & Rosenheim, 2013). Ecological filtering can, in addition, result in different species composition, and consequently differences in trait values (Outreman et al., 2018). Our study emphasised the role of environmental (climate and landscape) variables. It was not designed to test for phenotypic plasticity as a generator of intra-specific trait variation, since we focused on documenting inter-specific differences in traits. The effects of biotic interactions and intra-specific variability on parasitoid community characteristics require further study.

Land conversion to intensively managed croplands has led to global declines in the abundance and diversity of beneficial insects (Chaplin-Kramer et al., 2011; Kennedy et al., 2013). However, the resulting effects on pest control and crop yields are inconsistent and vary widely across crops and locations (Karp et al., 2018). The apparent disconnect between the abundance and richness of natural enemies and their pest control services may be resolved by understanding how local farm management interacts with their life-history traits. Our work emphasises the importance of looking at insect traits related to habitat conditions at the species level and suggests that investment in early developmental stages is an important strategy in highly disturbed anthropogenic systems.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTION

Miriam Kishinevsky and Tamar Keasar conceived the study, Miriam Kishinevsky conducted field and lab work, Miriam Kishinevsky and Tamar Keasar analysed the data and wrote the paper.

DATA AVAILABILITY STATEMENT

Upon acceptance of the manuscript, the study's raw data will be deposited at https://tamarkeasarlab.weebly.com/data-sets.html.

ORCID

Miriam Kishinevsky https://orcid.org/0000-0003-2633-7632

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Table S1 Supplementary tables.