



Habitat use by crop pests and natural enemies in a Mediterranean vineyard agroecosystem



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ABSTRACT

Conservation of natural habitats within agroecosystems often enhances the abundance and species diversity of arthropod natural enemies, but does not necessarily improve the biological control of crop pests. Differences in habitat use between some natural enemies (favoring natural areas) and pests (aggregating on the crop plants), were proposed to underlie low pest control in spite of high abundance of beneficials. To test this hypothesis, we characterized the habitat use of important vineyard pests (European grapevine moths and vine mealybugs) and of natural enemies (parasitoid wasps and spiders), and compared natural enemy communities across habitats. Arthropods were sampled in five vineyards (from vines and from herbaceous vegetation), and from adjacent natural habitats, using pheromone traps, visual searches and vacuuming. European grapevine moth and mealybug populations were highest inside the vineyards, furthest away from natural habitats. The proportion of natural enemies out of all arthropods was highest in the natural habitats. Parasitoid diversity was highest in natural habitats, intermediate on herbaceous vegetation within vineyards, and lowest on vines, and their abundance was higher on herbaceous vegetation than on vines. The parasitoids' distribution between natural and agricultural habitats varied among morpho-species, and their community composition differed among habitats and sampling dates. Spiders were less common than parasitoids (2.9% vs. 14.4% out of all suction-sampled arthropods, respectively), yet similarly distributed. As hypothesized, natural enemies associated with herbaceous vegetation more strongly than did grape pests, and their community composition differed between natural habitats and vineyards. To support the full diversity of beneficial arthropods, non-crop herbaceous vegetation both around and within vineyards should be conserved.

1. Introduction

Sustainable management of agricultural lands aims, among other applications, to protect biodiversity and advance ecosystem services. This approach involves reduced reliance on chemical control of agricultural pests while shifting towards biological control and integrated pest management practices (Dicks et al., 2013; Pretty et al., 2010). Measures to increase vegetation abundance and diversity in and around agricultural plots are frequently applied to encourage natural enemies of crop pests. These include conservation of native vegetation and

flowering plants on farmlands, conservation of nearby natural habitat, inter-cropping, annual cover crops or companion plants in the margins of agricultural plots (Dicks et al., 2013; Jonsson et al., 2008; Pretty et al., 2010). The increase in plant diversity is expected to reduce pest damage by disrupting herbivores from finding their host plants, by attracting pests to the non-crop vegetation, and by increasing resources (e.g., food and refuge) for natural enemies such as predatory and parasitic arthropods (Landis et al., 2000; Parker et al., 2013).

Indeed, the abundance and diversity of natural enemies often increases with plant diversity in agricultural plots and neighboring

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habitats (Langellotto and Denno, 2004; Letourneau et al., 2011) and with higher percentage of suitable non-crop habitats in the agroecosystem (Pluess et al., 2010). However, the effects of conservation measures on herbivore populations (Attwood et al., 2008; Straub et al., 2008) and on pest suppression (Chaplin-Kramer et al., 2011; Tschamntke et al., 2016) are complicated and not fully understood. In some studies, habitat diversification clearly reduced herbivore populations and crop damage (Bianchi et al., 2006; Tschumi et al., 2015). In others, increasing arthropod diversity through habitat manipulation had no discernible effect on pest populations within the agroecosystem (Kishinevsky et al., 2017; Martin et al., 2013). In yet other studies, habitat manipulations increased pest populations, as pests benefited from alternative resources provided by the non-crop plants more than their natural enemies (Danne et al., 2010; Letourneau et al., 2011). Furthermore, some habitat interventions enhanced negative interactions within assemblages of natural enemies, which resulted in reduced biological pest control (Winqvist et al., 2011).

An additional hypothesis for low pest control despite high abundance of beneficials is differential habitat use by pests and natural enemies, which limits their potential for predator-prey interactions. This might be the case if some natural enemies, which are attracted to non-crop habitats in agroecosystems, do not utilize the crop plants. Such species are likely to prey on herbivores in the non-crop vegetation, but not on agricultural pests that aggregate on the crop plants. In support of this hypothesis, crop fields and nearby natural habitats in France were found to harbor separate aphid-parasitoid food webs, which showed only little overlap (Derocles et al., 2014). Similarly, the light brown apple moth in Australia is attacked by two parasitoids, but only one of them inhabits vineyard habitats and provides pest control on the crop plants (Feng et al., 2017). The predictions generated by this hypothesis are (a) high abundance and diversity of natural enemies in non-crop vegetation, and high abundance of pests on crop plants; (b) different community compositions of natural enemies in non-crop vs. crop habitats. Here, we test these predictions for two crop pests and a large assemblage of natural enemies (parasitoid wasps and spiders) in a Mediterranean vineyard agro-ecosystem.

Several studies demonstrated the effects of non-crop vegetation on natural enemies in vineyards. Proximity of vineyards to natural and semi-natural vegetation increased parasitoid populations (Gaigher et al., 2015; Smith et al., 2015; Thomson and Hoffmann, 2013) and provided some species with overwintering habitat (Williams and Martinson, 2000; Zanolli and Pavan, 2011). Parasitism rates on some (Murphy et al., 1998; Thomson and Hoffmann, 2009; Wilson et al., 2015) but not all (Bell et al., 2006) agricultural pests also increased in vineyards that were close to natural habitats. It was also shown that the abundance and species richness of natural enemies in unmanaged vineyards are as high as in natural habitats (Gaigher et al., 2016).

Parasitoids vary in their habitat requirements, and therefore their community composition is affected by the type of non-crop vegetation that surrounds the vineyards (Thomson and Hoffmann, 2013) or that is used as cover crop under the vines (Danne et al., 2010). Similarly, the composition of spider assemblages is affected by landscape heterogeneity around the vineyards (Isaia et al., 2006) and differs between vineyards and natural areas (Gaigher and Samways, 2014). Plant-rich weedy margins of vineyards support populations of spiders and predatory insects such as ladybugs (Franin et al., 2016). Although spiders migrate from natural areas into vineyards (Hogg and Daane, 2010), their abundance and diversity within vineyards are not influenced by the percentage of surrounding natural habitat (D'Alberto et al., 2012; Gaigher and Samways, 2014).

Only two non-replicated pioneering studies investigated the distribution of both pests and their natural enemies among habitats within and around vineyards. In a vineyard in California that bordered a forest and was transected by a vegetation corridor, insect predators were most abundant on non-crop vegetation at the margins of the vineyard and close to the corridor, while the density of crop pests was highest at the

center of the plots (Nicholls et al., 2001). In another Californian vineyard, an island of flowering wild plants was established in the center of the plot. Predators and parasitoids were mostly found within and near the island, while the numbers of thrips (Thysanoptera) pests increased with increasing distance from the island (Altieri et al., 2005). These differences in distribution patterns were attributed to aggregation of natural enemies on the non-crop vegetation, which led to local suppression of pests in this habitat.

In the current study, we assessed the distribution of vineyard pests and of two important groups of natural enemies, within and near wine-producing vineyards. We improve on earlier investigations by using a spatially replicated design, and by comparing the community composition of natural enemies among crop- and non-crop habitats within the studied agroecosystem.

We focused on two key vineyard pests in Israel, the European grapevine moth (EGVM) *Lobesia botrana* (Denis and Schiffermüller, 1775) (Lepidoptera: Tortricidae), and the vine mealybug *Planococcus ficus* (Signoret, 1875) (Hemiptera: Pseudococcidae). EGVM is a polyphagous pest, native to Europe. It is a long-standing invasive pest of vineyards, persimmons, and pomegranates in Israel (Steinitz et al., 2015). The larvae of the moth feed on flowers and fruits of the host crops, causing direct damage and exposing the fruit to fungi and molds. Up to four generations may complete their development within a year. Currently, control of this pest combines pesticide applications with mating disruption using a synthetic version of the female sex pheromone (Gordon et al., 2005). Most of EGVM's reported natural enemies are generalist parasitoids of tortricids or related lepidopteran species, which specialize on one of the moth's pre-adult stages (egg, larva or pupa, Ioriatti et al., 2011). The vine mealybug is distributed in southern Europe, the Middle East and in parts of Africa, South America and North America (Daane et al., 2012). It is highly polyphagous, and develops on diverse crops including grapevines, figs, apples, citrus, avocado and mango. It has a high reproductive rate and produces 4–6 generations annually. The vine mealybug is considered a significant economic pest, mainly because it is a vector of the grapevine leafroll virus complex (Sokolsky et al., 2013). In addition, its honeydew secretions attract fungal pests. The mealybug develops on all parts of the plant, including the roots, where it is protected from insecticides. It has several effective natural enemies, including parasitoids, ladybeetles and antlions. The most important natural enemy of the vine mealybug in Israel is the parasitoid *Anagyrus* sp. nr. *pseudococci* (Girault, 1915) (Hymenoptera: Encyrtidae). Females of this parasitoid use the female sex pheromone of the vine mealybug females to locate their hosts (Franco et al., 2008), and can therefore be monitored using the pheromone traps that are installed for monitoring the pest. Several species of Cicadellidae are gradually becoming major vineyard pests, and are potential prey of parasitoids as well as of spiders. Because their taxonomy is poorly known, we were not able to provide a species-level description of their habitat use in this study.

2. Methods

2.1. Study sites

Five wine-producing vineyards in a Mediterranean agroecosystem in northern Israel were selected for the study (see Table S1 for locations). The area is characterized by Mediterranean climate, with cool winters and hot, dry summers. Annual rainfall is ca. 600 mm, mostly occurring between October and April. The soil is brown grumosol, and the prevalent wind direction is from north to south. The vineyards were planted with Cabernet Sauvignon vines. Each vineyard was six Hectare or larger in area and bordered a natural mixture of herbaceous vegetation and bush steppe on at least one side. Flowering herbaceous plants in the natural habitats were recorded at peak bloom (early April) and are listed in Table S2.

The grapes started flowering in April and were harvested in August.

The vineyards were treated with pesticides as recommended by an extension specialist during this period. Two hectares within each vineyard were additionally treated with mating disruption against the vine mealybug and EGVM. To this aim, dispensers with the female sex pheromones were hung in the treated plots in the first week of May. For the sake of the present analysis, we pooled the data from mating-disruption and no-mating-disruption control plots in each vineyard. The pesticides used, their application dates and the effects of mating disruption on pests and beneficial arthropods are reported in Shapira et al. (2018). All vineyards were treated with herbicides starting in mid-April. This resulted in a very low vegetation cover between the vine rows (< 2%) throughout the grape-growing season. The green vegetation cover in the natural habitats was 100% in spring, and gradually declined towards summer as annual plants dried. The vineyards were drip-irrigated from June until the harvest.

2.2. Arthropod sampling design

EGVM and vine mealybug males were sampled using pheromone traps. The dispensers and pheromone for EGVM were manufactured by Shin-Etsu (Tokyo, Japan). The dispensers and pheromone for the mealybugs were produced by Suttera (CheckMate VBM-XL; Suttera, Bend, OR, USA). Eight traps of each type were placed in each study site along two transects (Fig. 1, trapezoids): In the natural habitat adjacent to the vineyard (30–50 m into the natural vegetation), at the edge of the vineyard, at the center of the vineyard, and at the border between the focal vineyard and a neighboring vineyard (10, 60 and 100 m into the plot, respectively). Traps inside the vineyards were placed at equal distances from one another along each transect. The distances between the traps varied between vineyards, depending on the geometry and area of the plots. The compass directions of the natural habitats, relative to the agricultural habitat, varied among vineyards as well (Table S1). This variability is expected to reduce the effects of local wind directions on the dispersion of volatiles from the pheromone traps. Pheromone lures were replaced every 4 weeks. Traps were emptied at about monthly intervals during May–November. Vine mealybug males, EGVM and females of *Anagyrus* wasps found within the traps were

counted.

To assess the distribution of female vine mealybugs, we searched the stems, branches and fruit of 48 grapevines per vineyard. The sampled vines were located along eight planting rows. Within each row, we sampled the two adjacent vines closest to the natural habitat, two adjacent vines at the center of the vineyard and two adjacent vines at mid-distance between the natural habitat and the center (Fig. 1, pairs of vines are marked as circles with crosses). Each vine was searched for five minutes. The abundance of vine mealybugs of different life-stages (crawlers, juveniles and adults) per vine was scored using a discrete scale (0 – no mealybugs; 1 – 1–10 individuals; 2 – 11–30 individuals; 3 – > 30 individuals). Vine mealybug egg sacs were counted. Parasitized mealybugs were identified by the greyish color of the mummy or the parasitoid's exit hole.

To estimate infestation by EGVM, we inspected 100 grape bunches per vineyard for eggs, larvae and damaged berries in May, and again in July, shortly before the harvest. The bunches were sampled randomly from different areas in the vineyards.

Vegetation-dwelling arthropods were suction-sampled in May, July and September using a Vortis Insect Suction Sampler (Burkard Manufacturing Co. Ltd., Rickmansworth, UK). We collected six samples from the vine foliage, six samples from ground herbaceous vegetation between the vine rows and six samples from vegetation in a neighboring natural habitat, 50–100 m from each vineyard's edge (Fig. 1, full circles). Sampling locations were 20–50 m apart, depending on the density of green vegetation patches within the vineyards. Suction durations were 15 s/sample. The area covered per suction sample was adjusted to the vegetation density at the sampling point and ranged 1–3 m². Each sample collected from the herbaceous vegetation within the vineyards was followed by a sample collected from the nearest vine. Samples were stored in 75% ethanol and refrigerated until sorting.

2.3. Arthropod classification

Arthropods from the suction samples were classified at least to order level. Parasitoid wasps were classified to family or genus levels and were further sorted into morphospecies. Classification was based on

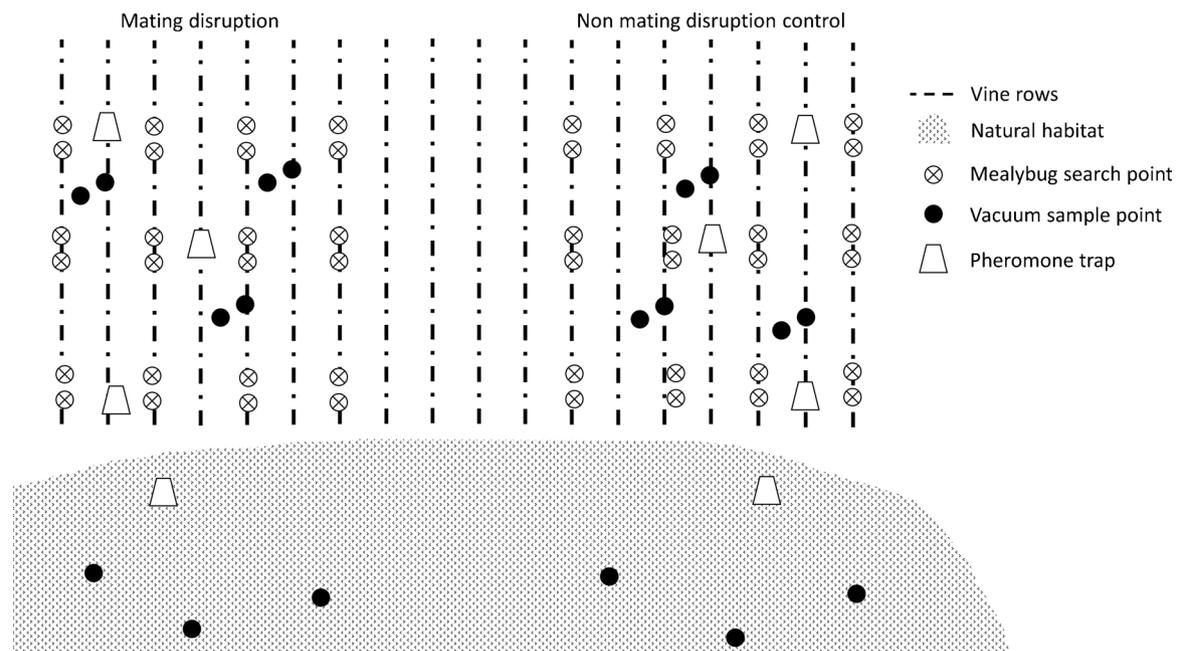


Fig. 1. Sampling locations within and near the vineyards. Dotted lines denote the wine rows. A plot treated with mating disruption against EGVM and vine mealybugs, and a control plot with no mating disruption, were sampled in each vineyard. Trapezoids: locations of pheromone traps; full circles: suction sampling locations; circles with crosses: locations of visual searches for mealybugs on vines. Each circle denotes two neighboring vines. Grape bunches were sampled for EGVM infestation at random locations within the vineyards. These sampling locations are not shown in the Figure.

Goulet and Huber (1993), Grissell 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). Spiders were identified to the family level, because 98.5% of all spiders were juveniles that could not be identified to genus or species level.

2.4. Data analysis

All arthropod counts were averaged across the replicate samples in each combination of vineyard, sampling location and month, to avoid pseudo-replication. Sampling locations for trap data were (1) natural habitat, (2) natural-vineyard border, (3) center of vineyard or (4) the border between two neighboring vineyards. For the visual search data, sampling locations were (1) the vineyard-natural area border, (2) the center of the vineyard or (3) the border between contiguous vineyards. For the suction data, sampling locations were defined as (1) vine foliage, (2) herbaceous vegetation between the vineyards' planting rows and (3) vegetation in the natural habitat. Sampling months were May–November for trap data (six time-points), and May, July and September for visual search and suction-sample data (three time-points). Thus, we analyzed 120 data points from trap-caught insects (5 vineyards \times 4 sampling locations \times 6 months) and 45 data points for arthropods monitored through visual search and suction sampling (5 vineyards \times 3 sampling locations \times 3 months).

2.4.1. Insects collected from pheromone traps

We divided the number of individuals in each trap at emptying by the number of days elapsed since the previous emptying of the trap. Multiplying this quotient by 100 provided the estimated number of captures/100 days/trap. This allowed us to treat the trap captures as count data with Poisson-distributed error in General Linear Mixed Models (see below).

2.4.2. EGVM and vine mealybugs from visual searches

Only seven EGVM larvae were found in all inspected grape bunches, therefore these data were not analyzed further.

2.4.3. General linear mixed models

The mean abundance values of arthropods were rounded to whole numbers, to allow modeling as count data with a Poisson error distribution. The mean scores of adult vine mealybugs and crawlers were first multiplied by 10, then rounded. This was done because the mean raw scores were consistently lower than 0.5, thus would have generated only 0 scores if simply rounded. We used GLMMs with Poisson link functions to test for the effects of sampling location (a fixed factor) and sampling month (a random factor) on the abundance of different arthropods. The models were constructed separately for data obtained from traps, from visual searches and from suction sampling. Site was added to the models as a random-intercept factor to account for the matching of the different sampling locations within each of the five studied vineyards, and to incorporate the variability among vineyards into the models. These full models were compared with reduced models, which did not include location as a factor. In a second set of reduced models, we excluded both sampling location and sampling month as factors. Likelihood ratio tests were conducted to compare the fit of the three models to the data.

2.4.4. Natural enemies

We combined the parasitoids, spiders and antlions collected in the suction samples into the functional group “natural enemies”. We calculated the proportions of natural enemies out of the total number of arthropods in each sample. The suction-collected parasitoids and spiders accounted for 98.7% of the natural enemies, leading us to analyze each of these two groups in greater detail.

Parasitoid morphospecies diversity and spider family diversity were

estimated using Shannon's index. We used Generalized Linear Mixed Models to test for the effects of the fixed factors habitat (vine, non-crop vineyard and non-crop natural) and month (May, July and September) on the square-root transformed proportions of natural enemies, and on the abundance and diversity of parasitoids and spiders. Site was included as a random-intercept factor in the models to account for the matching of the three habitats within each sampling site.

We used R software version 3.3.2 for the above-mentioned analyses (R Core team, 2016). GLMMs were run with the package lme4 (Bates et al., 2015).

Ordination methods with Canoco for windows 4.5 (ter Braak and Smilauer, 2002; Leps and Smilauer, 2003) were used to study and visualize the species and family compositions of the parasitoids and spiders. Canonical Correspondence Analysis (CCA) was performed (length of gradient was > 4) to test the effects of vineyard (both as main effect and as co-variable), habitat and month (as main effects) on the species composition of parasitoids. For spiders, redundancy analysis (RDA) was used (length of gradient was < 3) to examine the effects of vineyard (both as main effect and as co-variable), habitat and month (as main effects) on the family composition. Both analyses employed 4999 unrestricted Monte Carlo permutations.

3. Results

3.1. Numbers of collected arthropods

332 EGVM males, 912 mealybug males and 427 *Anagyrus* sp. nr. *pseudococci* parasitoids were recovered from the pheromone traps. 11,809 arthropods were collected in the suction samples. 14.4% and 2.9% of them were parasitoids and spiders, respectively.

3.2. Pests

The abundance of EGVM males was generally lowest in pheromone traps placed in the natural habitat and highest in the traps placed at the border between vineyards (i.e., furthest away from the natural areas, Fig. 2). Vine mealybugs of all developmental stages, sampled on the vines, and male vine mealybugs captured in pheromone traps, showed similar distribution patterns (Figs. 3a–c, 4 a). The abundances of EGVM and mealybugs (both on vines and in traps) also varied among sampling months, and thus were significantly affected by trapping location and season (Table 1). The frequencies of parasitized vine mealybugs (presumably by *Anagyrus* sp. nr. *pseudococci*) were low: 0.02 ± 0.01 near natural habitats, 0.02 ± 0.01 at the center of the plots and 0.004 ± 0.004 near neighbouring vineyards.

3.3. Natural enemies

The mean proportion of natural enemies out of all arthropods in the suction samples was highest in the natural habitat, especially in July (Fig. 5a, Table 1). Accordingly, it was significantly affected by habitat and month (Linear Mixed Model on square root transformed data: $F_{66,2} = 6.16$, $p = 0.003$ for habitat; $F_{66,2} = 4.02$, $p = 0.02$ for month). The distribution patterns of parasitoids and spiders (the most abundant natural enemies) among habitats are analysed in more detail in the paragraphs below.

3.3.1. Parasitoids

168 morpho-species of 18 families were identified. The total abundance of parasitoids per sample differed significantly among the three sampled habitats but not among sampling months. It was consistently lower on the grapevines than in the non-crop vegetation (Fig. 5b, Table 1).

Shannon's morphospecies-level diversity index was significantly affected by habitat and by sampling month (LMM: $F_{2, 65} = 44.98$, $p < 0.001$; $F_{2, 65} = 11.29$, $p < 0.001$, for habitat and month,

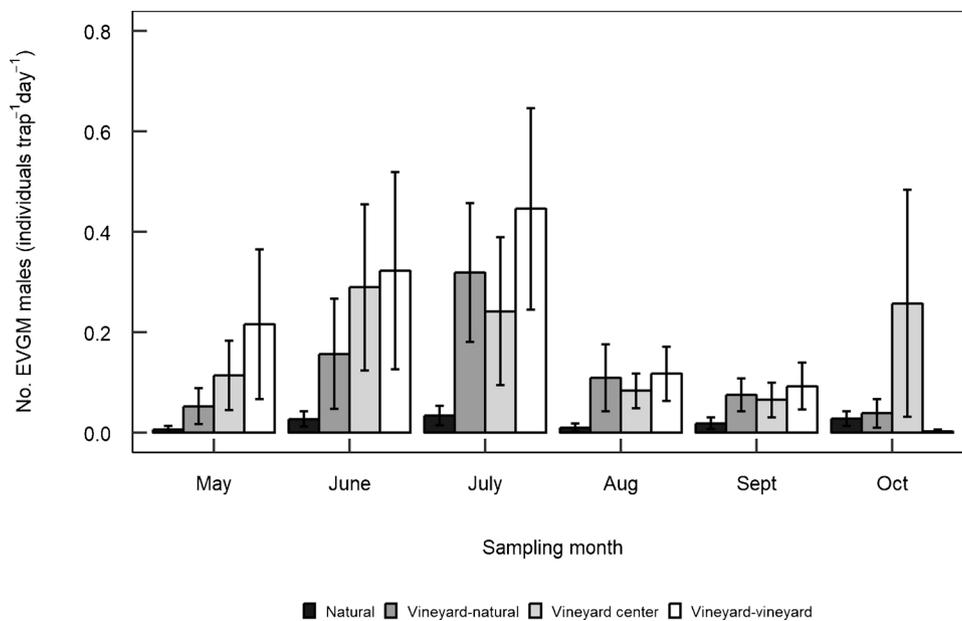


Fig. 2. Mean ± SE daily captures of EVGM males in pheromone traps.

respectively): it was highest in the natural non-crop vegetation, intermediate on non-crop vegetation within the vineyards, and lowest on the grapevines. The wasps' diversity also decreased from May to September (Fig. 5c).

The composition of parasitoid species in the suction samples was significantly affected by vineyard, habitat and month (Table 2). As variation between vineyards was high, we added vineyard as co-variable to the analysis. Fig. 6a visualizes the parasitoid species composition in grapevines with vineyard as co-variable, and with habitat and month treated as main effects. The parasitoid composition in the

natural habitat differed significantly from that of the agricultural habitat, while the herbaceous vegetation within the vineyard and the vines contained similar parasitoid communities. Parasitoid composition also varied significantly between months (Table 2).

Fourteen species of parasitoids were relatively common (> 20 individuals in all samples combined). These species were identified to genus level and classified to guilds according to their putative hosts, based on literature records (Table S3). Their abundance in respect to habitat and sampling month is depicted in Fig. 6a. Interestingly, two common putative parasitoids of Lepidoptera (*Telenomus* sp1 and

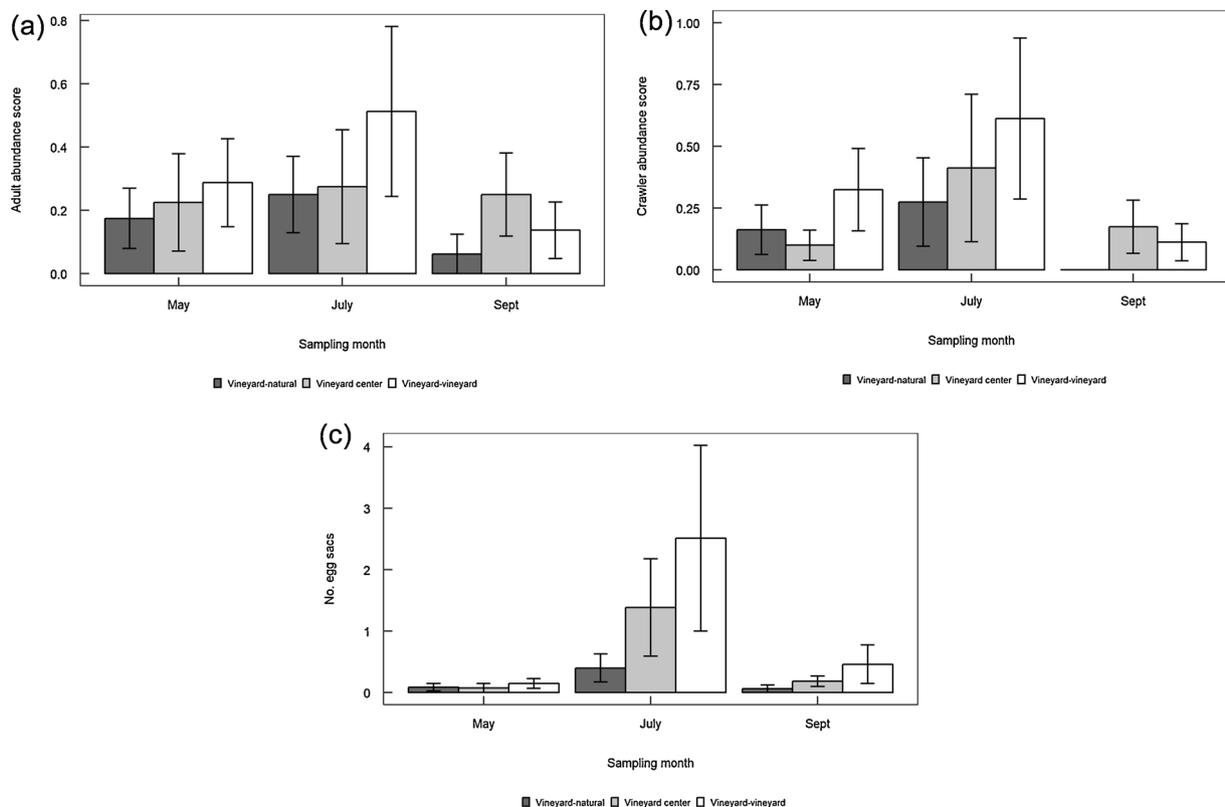


Fig. 3. Mean ± SE abundance of grapevine mealybugs sampled per vine. (a) adult abundance score, (b) crawler abundance score, (c) number of egg sacs.

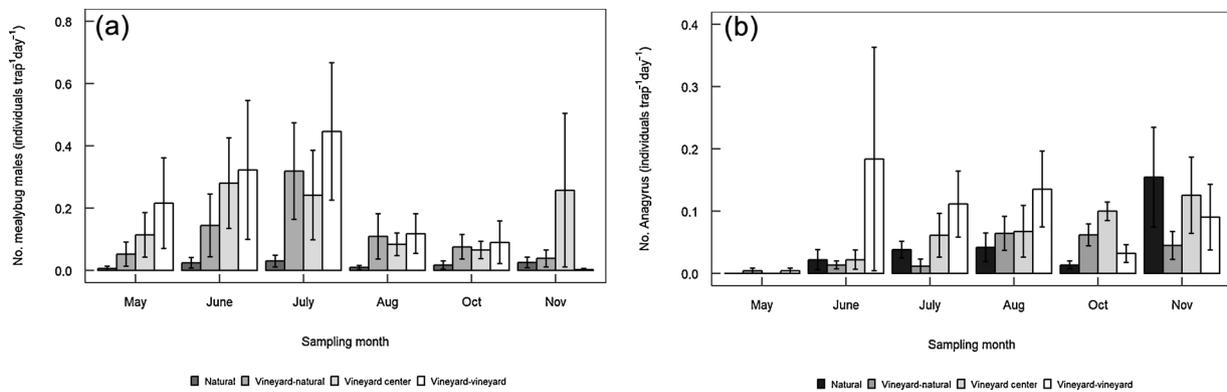


Fig. 4. Mean ± SE daily captures of grapevine mealybug males (a) and the parasitoid *Anagyrus* sp. nr. *pseudococci* (b) in pheromone traps.

Telenomus sp2: Platygastridae) occurred in similar numbers in natural as in agricultural habitat. The species most clearly associated with the natural habitat were parasitoids of leafminers (*Neochrysocharis formosus* and *Cirrospilus* sp.).

Anagyrus sp. nr. *pseudococci* parasitoids were counted in the vine mealybug pheromone traps, as they are attracted to their host’s sex pheromone. They were more abundant in the agricultural habitat than in the natural habitat throughout most of the season but were mainly trapped in the natural habitat in November. Accordingly, their abundance was affected both by trap location and by sampling month (Fig. 4b, Table 1).

3.3.2. Spiders

98.5% of the collected spiders were juveniles. Only four adult females and one adult male spider were sampled. Of the 330 spiders collected, 318 were identified to family level, representing 12 spider families. Six spider families were represented by more than 20 individuals (Salticidae, Philodromidae, Thomisidae, Linyphiidae, Araneidae and Theridiidae, Table S4). The abundance (Fig. 7a) and family-level diversity (Fig. 7b) of spiders were generally higher in non-crop vegetation than on the vines. Habitat and sampling month significantly affected spider abundance (Table 1) and diversity ($F_{2, 47} = 9.75, p < 0.001$ for habitat, $F_{2, 47} = 5.17, p = 0.009$ for month).

Similar to the parasitoid community, the spider family composition was significantly affected by vineyard, habitat and month (Table 2). As variation between vineyards was high, we also analyzed the spider composition with vineyard as co-variable (Fig. 6b). The main effects, habitat and month, remained statistically significant. The spiders’ family-level composition differed significantly between the natural and agricultural habitats, but not between vines and the herbaceous vegetation within the vineyards (Table 2).

4. Discussion

In agreement with our working hypothesis and with previous

studies (Nicholls et al., 2001; Altieri et al., 2005), major vineyard pests and most of the natural enemies showed little overlap in habitat use during the fruit-growing season (May–July). Vine mealybug female counts, as well as numbers of vine mealybug and EGVM males in pheromone traps, were highest away from the natural area. In contrast, the abundance of natural enemies was highest on natural herbaceous vegetation between the vines, and in the natural habitats bordering the vineyards. The diversity of natural enemies was highest in the natural habitats, possibly because of their higher plant cover, more diverse herbivore prey and lower pesticide exposure compared to the vineyards. This pattern was also observed in the post-harvest samples (September), when agricultural activity within the vineyards was much lower than pre-harvest. These results, like similar studies in other vineyard agroecosystems, suggest that non-crop herbaceous vegetation helps sustain arthropod predators and parasitoids (Loni et al., 2014; Shapira et al., 2017).

Habitat also affected the composition of the natural enemies. In line with our hypothesis, species composition of parasitoids and family composition of spiders differed between the natural and the agricultural habitats. Therefore, to support the whole diverse assemblage of beneficial arthropods, herbaceous vegetation in both habitats should be conserved (Gaigher et al., 2015). Species that inhabit the vineyards are likely to play a larger role in pest control than species that specialize in the natural habitat. Habitat preferences of natural enemies that could potentially attack the major grapevine pests (parasitoids of Lepidoptera and mealybugs) are of special interest. These included two species of *Telenomus* (Platygastridae), a genus that attacks lepidopteran and heteropteran eggs. Interestingly, these species were not strongly associated with either agricultural or natural habitat and may parasitize different hosts in each habitat. Similarly, the parasitoid *Anagyrus* sp. nr. *pseudococci* (Encyrtidae), an important natural enemy of mealybugs, was sampled within the vineyards along the summer, but its abundance in the natural habitat increased towards the winter. These findings suggest that potential biocontrol agents in our agroecosystem use the non-crop vegetation both within and outside of the vineyards. It is yet unknown

Table 1

The effects of sampling location and month on the abundance of arthropods sampled in the study. Results of likelihood ratio tests for comparisons of Linear Mixed Models are reported.

Arthropod	Sampling method	Effect of sampling location	Effect of sampling month
EVGM	Pheromone traps	$\chi^2 = 1103.1, df = 3, p < 0.001$	$\chi^2 = 1234.0, df = 2, p < 0.001$
Vine mealybug:			
Adult females	Visual search	$\chi^2 = 6.61, df = 2, p = 0.04$	$\chi^2 = 12.97, df = 2, p = 0.002$
Crawlers	Visual search	$\chi^2 = 12.69, df = 2, p = 0.002$	$\chi^2 = 36.48, df = 2, p < 0.001$
Egg sacs	Visual search	$\chi^2 = 12.73, df = 2, p = 0.002$	$\chi^2 = 36.58, df = 2, p < 0.001$
Adult males	Pheromone traps	$\chi^2 = 567.45, df = 3, p < 0.001$	$\chi^2 = 606.38, df = 2, p < 0.001$
Parasitoids	Suction	$\chi^2 = 112.36, df = 2, p < 0.001$	$\chi^2 = 0.08, df = 2, p = 0.96$
<i>Anagyrus</i> sp nr. <i>pseudococci</i>	Pheromone traps	$\chi^2 = 89.98, df = 3, p < 0.001$	$\chi^2 = 351.76, df = 1, p < 0.001$
Spiders	Suction	$\chi^2 = 12.55, df = 2, p = 0.002$	$\chi^2 = 7.61, df = 1, p = 0.006$

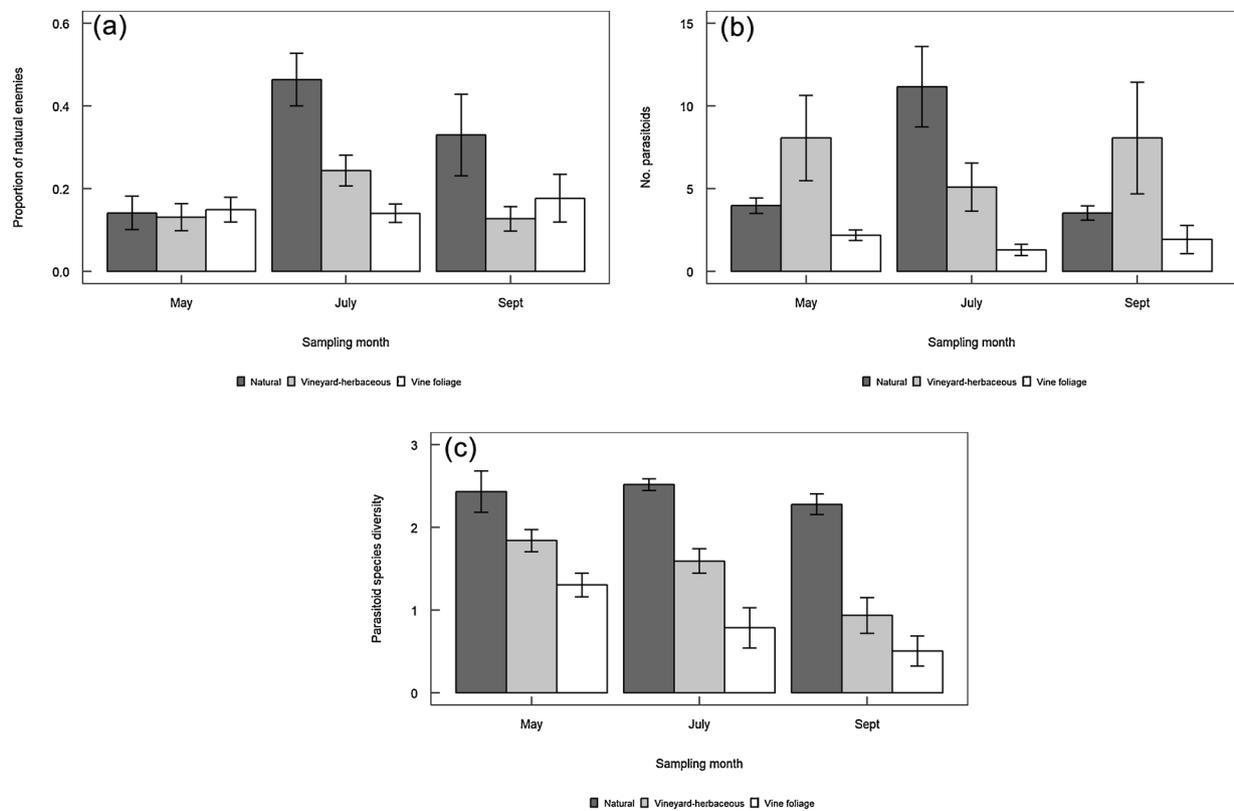


Fig. 5. (a) The proportions of potential natural enemies (parasitoids, spiders and antlions), out of the total arthropods in the suction samples, (b) Mean + SE number of parasitoids per suction sample, (c) Mean + SE Shannon's diversity index for morphospecies of parasitoid wasps.

whether the two habitats provide similar resources (such as hosts), or whether parasitoids migrate between the natural and agricultural habitats to meet different requirements (e.g., hosts vs. sugar sources, Kishinevsky et al., 2018).

We also found that species of natural enemies may vary in habitat preference although they share the same foraging guild. For example, two common species of leafminer parasitoids (*Neochrysocharis formosus* and *Cirrospilus* sp.) were mostly found in the natural habitat, while a third species (*Diglyphus isaea*) was more frequent within the vineyards. Similarly, a few families of web-building spiders (such as Araneidae) were sampled mainly in the natural areas while the web-building family Linyphiidae characterized the agricultural habitat. This variability possibly reflects subtle differences between species in their reaction to prey abundance, host-plant traits, agricultural management practices or

agricultural habitat (Samu and Szinetár, 2002; Gavish-Regev et al., 2008; Pluess et al., 2008; Kishinevsky et al., 2016).

Spider and parasitoid populations differed in their seasonal trends. While parasitoid abundance was not affected by sampling season, spiders declined in September. None of the spider families were significantly associated with the September samples, whereas these samples were characterized by a distinct assemblage of parasitoids. The lower abundance of spiders in the September samples may reflect population declines but could also result from a sampling artifact. Our suction sampler captures juvenile spiders more effectively than adult individuals. Possibly, a high proportion of spiders (which usually have one to two generations per year) reached adulthood by September. This could have reduced our efficiency in capturing them through suction sampling. In support of this interpretation, pitfall traps that were placed

Table 2
Summary of ordination analyses.

Dependent variable	Main effects	Co-variables	Variable values that differed significantly from the others	Percent of variation explained
Parasitoid community composition	Vineyard	None	Yiftach: F-ratio = 1.75, $p = 0.0002$ Mamman: F-ratio = 1.64, $p = 0.0014$ Bar West: F-ratio = 1.35, $p = 0.02$	26.8%
	Habitat Month		Natural: F-ratio = 2.14, $p = 0.0002$ May: F-ratio = 1.89, $p = 0.0002$ September: F-ratio = 2.88, $p = 0.0002$	
Parasitoid community composition	Habitat Month	Vineyard	Natural: F-ratio = 2.00, $p = 0.0002$ May and July: F-ratio = 2.15, $p = 0.0002$ September: F-ratio = 2.80, $p = 0.0002$	43.3%
Spider community composition	Vineyard	None	Dishon: F-ratio = 5.64, $p = 0.001$ Mamman: F-ratio = 2.51, $p = 0.03$	14%
	Habitat Month		Natural: F-ratio = 2.42, $p = 0.02$ May: F-ratio = 8.47, $p = 0.0002$	
Spider community composition	Habitat Month	Vineyard	Natural: F-ratio = 2.20, $p = 0.04$ May: F-ratio = 7.40, $p = 0.0002$ July, September: F-ratio = 2.39, $p = 0.04$,	9%

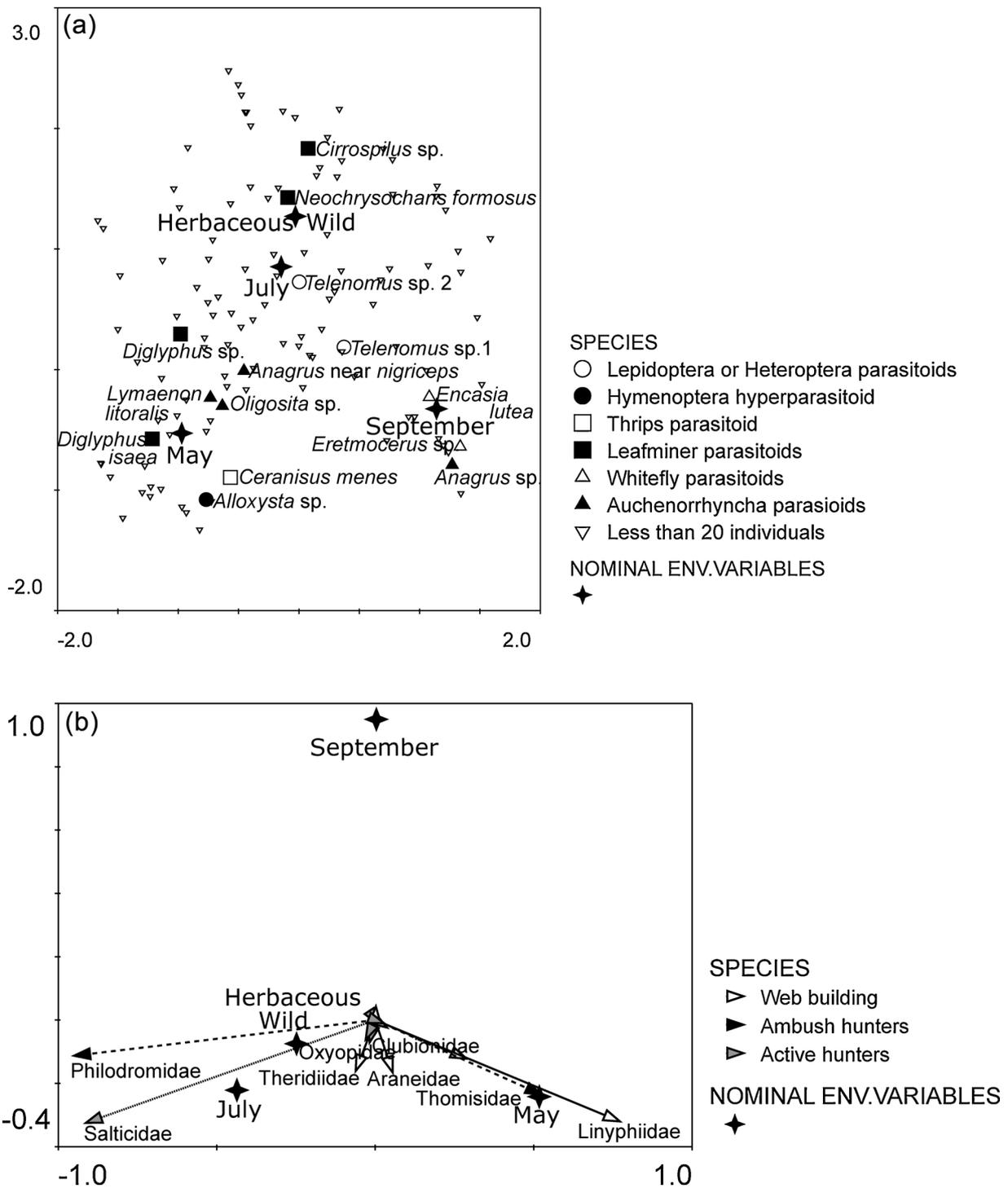


Fig. 6. (a) An ordination diagram from a Canonical Correspondence Analysis (CCA) of the composition of 168 parasitoid species, with habitat and month as significant main effects (represented as red triangular centroids) and vineyard as co-variable. Species with fewer than 20 individuals are represented by blue dots. Species with more than 20 individuals were assigned to guilds (each indicated by different symbol) by their putative hosts and are identified to genus. (b) An ordination diagram from a redundancy analysis (RDA) of 12 spider families and the composition in vineyards and neighboring natural areas. Habitat and month are significant main effects (represented as red triangular centroids) and vineyard was modeled as a co-variable. Families with fewer than six individuals are represented by arrows without their names, families with more than six individuals were assigned to three spider guilds: Web building spider families (represented by arrows: Linyphiidae, Araneidae, Theridiidae); Ambush hunter spider families (represented by red arrows: Philodromidae, Thomisidae); Active hunter spider families (represented by brown arrows: Salticidae, Oxyopidae, Clubionidae). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

in the experimental vineyards in parallel to the suction sampling captured much higher numbers of adult spiders (data not shown).

The higher abundance of parasitoids and spiders sampled from vegetation in the natural habitats bordering the vineyards, and the higher

abundance of vine mealybugs and EGVM away from the vineyard margins, could indicate that these pests are effectively controlled where natural enemies reach high densities (Nicholls et al., 2001; Altieri et al., 2005). We cannot evaluate this possibility because we do not know the

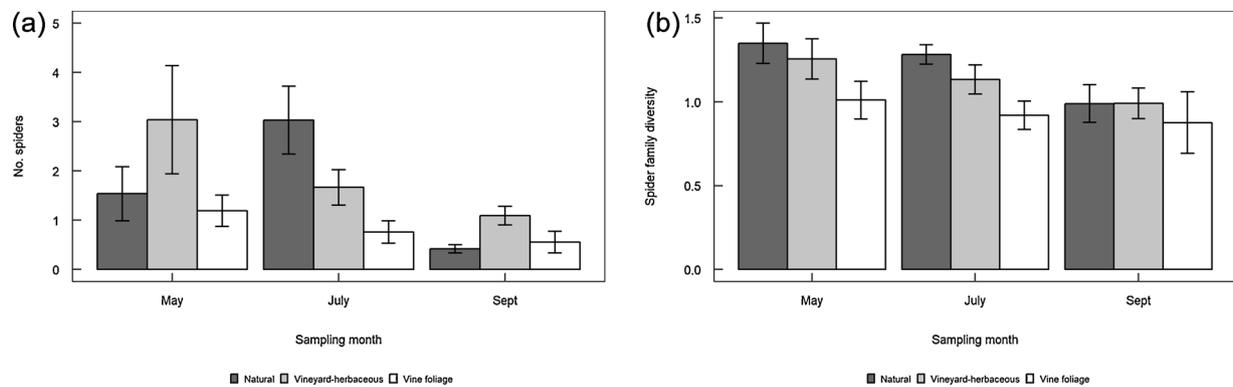


Fig. 7. Mean + SE abundance (a) and Shannon's diversity index for families (b) of spiders per suction sample.

host range of most of the sampled parasitoids, nor their parasitism rates. However, in the only case where we do have information on parasitism rates (*Anagyrus* sp. nr. *pseudococci* on vine mealybugs), it was lowest at the border between two vineyards, although this area had the highest abundance of hosts. A second interpretation of the different distribution of pests vs. natural enemies is that parasitoids and predators benefitted more from the resources in the natural habitat than did the crop pests. Such resources might include sugar sources (Kishinevsky et al., 2018), alternative hosts (Parker et al., 2013) or mere physical refuge. Our findings agree with a large meta-analysis that found higher abundance of arthropod predators and decomposers, but not of herbivores, on native vegetation than on agricultural crops (Attwood et al., 2008).

In conclusion, we found higher use of non-crop vegetation by natural enemies than by crop pests in our Mediterranean vineyard agroecosystem study sites. Moreover, the herbaceous plants within the vineyards and in nearby natural areas attracted different communities of beneficial arthropods. These findings advance our understanding of the complex interplay between habitat management, diversity of natural enemies and control of crop pests in agro-ecosystems.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2018.08.012>.

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