Aphid’s parasitoid fauna and their trophic associations in the oasis ecosystems of Zibans (Biskra, Algeria)

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Abstract
A study on the fauna of aphids’ parasitoids was carried out in the oasis ecosystems of the Ziban in the region of Biskra, Algeria. Eighteen primary parasitoids species belong to 2 subfamilies; Aphidiinae (Hymenoptera: Ichneumonoidea, Braconidae), represented by 17 species and 6 genera (Aphidius, Diaeretiella, Ephedrus, Lysiphlebus, Praon, and Binodoxys) and the subfamily Aphelininae (Hymenoptera: Chalcidoidea, Aphelinidae), represented by only one species of the genus Aphelinus was listed. The parasitoid species were collected and identified in association with 22 species of aphids infesting 29 host plant species belonging to 13 botanical families. A number of 83 tri-trophic plant-aphid-parasitoid associations were presented. The two parasitoid species, Aphidius matricariae (Hal.) and Lysiphlebus testaceipes (Cress.), were the most abundant species. The present study dealt only with primary parasitoids, while hyperparasitoids will be presented in another publication.

Keywords: Aphids, Parasitoids’ fauna, Survey, Oasis ecosystems, Biskra, Algeria

Background
Aphids (Hemiptera: Aphididae) are considered among the most important insect pests in agriculture that cause several damages. One of these damages is virus transmission (Glinwood 1998). Aphids’ control is more easy with the application of the insecticides; however, the misuse of these products possesses many problems.

Currently, in the face of observed ecological disorders, biological control is regarded as the most promising tool and strategy for sustainable agriculture as it has economic and ecological advantages. In applied entomology, the entomophagous auxiliaries used in biological control are mainly grouped into 2 categories: predators and parasitoids.

Aphids are attacked by 2 groups of hymenopteran parasitoids, Aphidiinae (Ichneumonoidea: Braconidae) and Aphelinidae (Chalcidoidea). Aphidiinae species are the most abundant and active ones in regulating of the aphid populations (Glinwood 1998). This subfamily contains 400 species all over the world parasitize exclusively aphids (Žikić et al. 2017).

Parasitoids play a main function in terrestrial food webs (Khan et al. 2012) and the study of these webs can provide an essential foundation to improve the effectiveness and comprehension of the decrease of herbivore populations by their natural enemies. For this reason, tri-trophic associations (plant-aphid-parasitoid) have benefited from many studies in several countries (Kavallieratos et al. 2004; Khan et al. 2012; Rakhshani et al. 2012). The fauna of parasitoids in Algeria has attracted great attention in recent years. Several studies have been conducted in different ecosystems; agricultural, natural environments, and urban environments. The eastern part of the country is the most affected region by these studies (Laamari et al. 2012; Hemidi et al. 2013; Tahar Chaouche and Laamari 2015; Aggoun et al. 2016). In the western part of Algeria (North-West), some studies have been conducted by Ghelamallah et al. (2018). In the North, in the littoral and sub-littoral region, this fauna has been inventoried by Aroun (2015). At the level of the Algerian Sahara, a study was conducted in the oasis regions by Chehma and Laamari (2014).

The objective of this study was to evaluate the structure of the aphid-parasitoid community in an agroecosystem with a functioning close to natural ecosystems; it is the oasis ecosystem which contains a large genetic diversity.
Materials and methods

Study area
The study was carried out in the region of Biskra, located in Northeastern Algeria. It forms a region of morphological and bioclimatic transition between the Northern mountainous area and the Southern Saharan highlands. It covers an area of 21,671.2 Km², with an altitude of 124 m.

The total area intended for agriculture (SAT) is about 1,652,751 ha, represents 77% of the total surface of the district.

The agricultural sector in the Ziban region is characterized by the predominance of an oasis mode of exploitation. These ecosystems are essentially based on date palm cultivation, which has been practiced in this region for centuries.

Climatically, Biskra is characterized by a hot and very dry summer, cold winter with subfreezing temperatures. During the period of study (March–June of 2014, 2015 and 2016), the average temperatures were respectively (22.1, 24.3 and 24.4°C), while correspondence averages of precipitation were 5, 7.5 and 22.5 mm, respectively.

The study was carried out in the oasis ecosystems of the Ziban region of Biskra. Three oasis farms were prospected, belong to different oasis systems existing in the region; a farm located at the municipality of Foughala (Zeb El Gherbi), the second at El Zeb El Chergui in the municipality of Chetma, and the third in the mountain oasis system that belongs to the municipality of Branis.

Sampling
Surveys were conducted weekly at all sites during the period of study (March–June). Two oasis farms (Foughala and Branis) were monitored in 3 consecutive years: 2014, 2015 and 2016, while the other farm (Chetma) was monitored in 2015 and 2016 only. Samples were collected when parasitoids and aphid host populations are well established in the palm groves. All the strata of the oasis system were sampled, these samples composed of parts of the infested plants “leaves, inflorescences, and young shoots”. A total of 200 samples were collected from all 3 sites.

Samples from different host plants bearing aphid colonies of both live and mummified aphids were carefully cut off and transferred to the laboratory. Live aphids were preserved in ethanol at 70% for identification, mummified aphids of the same species were placed with small parts of the same host plant(s) in small plastic boxes. On the lid of each box, there was a circular opening covered with muslin for ventilation in order to maintain inside the boxes similar conditions to those existing in the growth cabinet (22.5 °C, 65% RH, 16:8 L:D). Aphid mummies were inspected daily to determine freshly emerged adults of parasitoids. Those were then transferred by a fine brush into tubes containing 70% ethanol for further identification in the laboratory. Microscopic slides of parasitoids and dissected females’ adults were mounted in Eukit.

In the case of finding the aphids’ mummies only, the host aphid species was recorded as unknown in Table 1.

The identification of aphids and plants was made by Professor Malik Laamari at the Laboratory of Agronomy, Department of Batna (Algeria). The identification of hymenopteran parasitic species was carried out by the assistance of Dr. Souad Tahar Chaouch (Department of Agronomy, University of Biskra, Algeria) and based on several identification keys, in particular, those of Tomannovic et al. (2003a, b); Kavallieratos et al. (2004) and Talebi et al. (2009). The identification criteria were based on external morphology. The specimens identified were deposited in the laboratory of the Agronomy Department, University of Batna (Algeria).

Results and discussions
Surveys were carried out in the 3 palm groves belonging to the oasis ecosystem of the Biskra region during the 3 years of sampling (2014, 2015, and 2016) revealed the presence of 18 species of primary parasitoids collected from the mummies of 22 species of aphids collected from 29 plant species, belonging to 13 botanical families. A number of 83 plant-aphid-parasitoid tri-trophic associations were obtained in the study area. The species *Aphidius matricariae* (Hal.) was the most abundant species by 16 tri-trophic associations. As well, the species *L. testaceipes* formed 14 associations.

Distribution
About 37 species of the aphid parasitoids have been recorded in Algeria before (Laamari et al. 2011, 2012; Aroun 2015; Ghelamallah et al. 2018). In this study, 18 species of the primary aphid parasitoids recorded belong to the 2 subfamilies; Aphidiinae (Hymenoptera: Ichneumonoidea, Braconidae), represented by 17 species and 6 genera (*Aphidius, Diaeretiella, Ephedrus, Lysiphlebus, Praon*, and *Binodoxys*) and the subfamily Aphelininae (Hymenoptera: Chalcidoidea, Aphelinidae) represented by only one species of the genus *Aphelinus*.

Most of the species mentioned in this study (*Aphelinus mali*, *Aphidius colemani*, *A. ervi*, *A. funebris*, *A. matricariae*, *A. sonchi*, *Binodoxys angelicae*, *Diaeretiella rapae*, *Ephedrus niger*, *Lysiphlebus confusus*, *L. fabarum*, *L. testaceipes*, *Praon voluce*, and *P. yomenae*) have been already reported in Algeria (Laamari et al. 2011, 2012). They have not been found only in the countries of the Great Maghreb (Stary and Sekkat 1987; Ben Halima and Ben Hamouda 2005; Laamari et al. 2011, 2012; Boukhris-Bouhachem 2011; Ayadi et al. 2017) but also been found in the eastern Mediterranean region (Kavallieratos et al. 2004). According
Table 1  Tri-trophic associations, plant-aphid-parasitoid, noted at the oasis ecosystems in the region of Biskra between 2014 and 2016

| Parasitoids                      | Parasitized aphid species                      | Host plant                  |
|----------------------------------|------------------------------------------------|-----------------------------|
| *Aphelinus mali* (Haldeman, 1851) | *Hyperomyzus lactucae* (Linnaeus)              | *Sonchus oleraceus*         |
| *Aphidius colemani* (Viereck, 1912) | *Uroleucon compositae* (Theobald)              | *Centaurea* sp.             |
|                                  | *Hyalopterus pruni* (Geoffroy)                  | *Prunus armeniaca*         |
|                                  | *Aphis punicae* (Passerini)                     | *Punica granatum*           |
| *Aphidius ervi* (Haliday, 1834)  | *Uroleucon ambrosiae* (Thomas)                 | *Taraxacum officinale*      |
|                                  | *Uroleucon ambrosiae* (Thomas) mixed with       |                             |
|                                  | *Hyperomyzus lactucae* (L.)                    |                             |
|                                  | *Uroleucon sonchi* (L.)                        | *Sonchus oleraceus*         |
|                                  | *Unknown*                                      | *Capsella bursa-pastoris*   |
|                                  | *Rhopalosiphum maidis* (Fitch)                  | *Vicia faba*                |
|                                  | *Uroleucon sonchi* (L.) mixed with              | *Hordeum vulgare*           |
|                                  | *Hyperomyzus lactucae* (Linnaeus)              |                             |
|                                  | *Uroleucon ambrosiae* (Thomas)                 | *Taraxacum officinale*      |
|                                  | *Hyperomyzus lactucae* (Linnaeus)              | *Sonchus oleraceus*         |
|                                  | *Acythosiphon lactucae* (Passerini)             | *Lactuca serriola*          |
|                                  | *Capiptothorus inulae* (Passerini)              | *Coronilla scorpioides*     |
|                                  | *Ovatus inulae* (Walker)                       | *Polygonum aviculara*       |
|                                  | *Uroleucon sonchi* (L.)                        | *Launaea nudicaulis*        |
|                                  | *Therioaphis langloisi* (Remaudière & Leclant)  | *Hordeum vulgare*           |
|                                  | *Unknown*                                      | *Sonchus oleraceus*         |
|                                  | *Unknown*                                      | *Taraxacum officinale*      |
|                                  | *Unknown*                                      | *Dittrichia viscosa*        |
|                                  | *Unknown*                                      | *Dittrichia viscosa*        |
|                                  | *Unknown*                                      | *Dittrichia viscosa*        |
|                                  | *Aphis rumicis* (Linnaeus)                     | *Rumex* sp.                |
|                                  | *Brachycaudus rumexicolors* (Patch, 1917)      | *Rumex* sp.                |
|                                  | *Aphis acetosae* (Linnaeus)                    | *Rumex* sp.                |
|                                  | *Uroleucon ambrosiae* (Thomas)                 | *Taraxacum officinale*      |
|                                  | *Unknown*                                      | *Dittrichia viscosa*        |
|                                  | *Unknown*                                      | *Avena sativa*              |
|                                  | *Metopolophium dirhodum* (Walker)              | *Hordeum vulgare*           |
|                                  | *Uroleucon sonchi* (L.)                        | *Sonchus oleraceus*         |
|                                  | *Unknown*                                      | *Launaea nudicaulis*        |
| Parasitoids | Parasitized aphid species | Host plant                  |
|-------------|---------------------------|-----------------------------|
| Aphis gossypii (Glover) |  | Pyrus communis          |
| Unknown     |  | Malus domestica         |
| Unknown     |  | Taraxacum officinale   |
| Aphis pomi (De Geer) |  | Malus domestica        |
| Unknown     |  | Lactuca sativa         |
| Capitophorus inulae (Passerini) |  | Dittrichia viscosa  |
| Hyperomyzus lactucae (Linnaeus) |  | Sonchus oleraceus |
| Binodoxys angelicae (Halliday, 1833) | Aphis rumicis (Linnaeus) | Rumex sp.                  |
| Binodoxys sp | Aphis punicae (Passerini) | Punica granatum        |
| Diaeretiella rapae (M’Intosh, 1855) | Hyadaphis foeniculi (Passerini) | Rubia tinctorum   |
| Ephedrus niger (Gautier, Bonnamour & Gaumont, 1929) | Capitophorus inulae (Passerini) | Dittrichia viscosa  |
| Lysiphlebus confusus (Treemblay & Eady, 1978) | Ovatus inulae (Walker) | Dittrichia viscosa  |
| Lysiphlebus fabarum (Marshall, 1896) | Aphis fabae (Scopoli) | Solanum nigrum       |
| Rhopalosiphum maidis (Fitch) | Aphis fabae (Scopoli) | Hordeum vulgare     |
| Aphis craccivora (Koch) | Aphis craccivora (Koch) | Medicago sativa       |
| Capitophorus inulae (Passerini) | Capitophorus inulae (Passerini) | Dittrichia viscosa  |
| Aphis punicae (Passerini) | Aphis punicae (Passerini) | Punica granatum  |
| Aphis gossypii (Glover) | Aphis gossypii (Glover) | Malus domestica     |
| Dysaphis plantaginea (Passerini) | Dysaphis plantaginea (Passerini) | Malus domestica  |
| Rhopalosiphum maidis (Fitch) | Rhopalosiphum maidis (Fitch) | Hordeum vulgare   |
| Aphis fabae (Scopoli) | Aphis fabae (Scopoli) | Chenopodium album   |
| Unkonwn     | Unkonwn                   | Chenopodium murale    |
| Unkonwn     | Unkonwn                   | Portulaca oleracea    |
| Unkonwn     | Unkonwn                   | Solanum nigrum      |
| Praon sp. 1 | Uroleucon ambrosiae (Thomas) | Taraxacum officinale |
| Praon sp. 2 | Capitophorus inulae (Passerini) | Dittrichia viscosa |
| Praon sp. 3 | Aphis acetosae (Linnaeus) | Rumex sp.            |
| Praon volucre (Halliday, 1833) | Hyperomyzus slactucae (Linnaeus) | Lactua serriola  |
to Laamari et al. (2012), the parasitoid fauna of Algeria reveals a clear resemblance to that of southern Europe.

Based on the number of species identified up to the present study, and given the great taxonomic, ecosystemic and landscape diversity in Algeria, it could be, fairly, stated that further expended surveys of aphid parasitoids of the country will undoubtedly enrich the present list.

**Tri-trophic relationships: parasitoids-aphids-plants**

All Aphidiinae species having a high degree of specialization against aphids and important capacity to control these pests. This strong specialization is an advantage for biological control. For the effective use of these organisms in biological control, it is important to know the trophic relationships between parasitoid species, aphid species, and host plants. According to Navasse (2016), the study of plant-aphid-parasitoid food webs enables us to define locally the width of the host/parasitoid spectrum, the dynamics of temporal exploitation of hosts and the distribution of generalist and specialist species in the different habitats over time.

In the present study, the 2 species *A. matricariae* and *L. testaceipes* were the most abundant species among aphid parasitoids in terms of trophic relationships. The same observations were reported by Tahar Chaouche and Laamari (2015) in the natural environment of the same region, and by Laamari et al. (2011, 2012) in Eastern Algeria.

The species *A. matricariae* had 16 associations, parasitizing 10 species of aphids infest 10 plant species (Table 1). According to the present work and the works carried out by Tahar Chaouche and Laamari (2015) in the natural environment, by Hemidi et al. (2013) in the urban environment of the Biskra region, and Laamari et al. (2011, 2012), it could be stated that this parasitoid species has a broad spectrum of hosts in this region. It was found associated with 25 species of aphids. In the Eastern part of the country, it was recorded on 23 aphid species (Laamari et al. 2011), while in the North, it was found associated with 36 species (Aroun 2015). It was, also, reported as the dominant species in the western part (Ghelamallah et al. 2018).

The species *L. testaceipes* ranked the second, with 14 associations. It was collected from the mummies of 10 aphid species infested 12 plant species (Table 1). Currently, the host spectrum of this species is 13 species of aphids (Hemidi et al. 2013; Tahar Chaouche and Laamari 2015). It is reported in different types of habitats (natural, cultivated, and urban) and on different host plant species (spontaneous, cultivated, and ornamental plants). According to Laamari et al. (2011), this parasitoid was recorded parasitizing 20 aphid species.

This parasitoid originally from the Nearctic realm (Tomanović et al. 2018) introduced into France, and later became the most dominant parasitoid in the Mediterranean region (Žikic et al. 2015). The same authors mentioned that this parasitoid was recently classified as an invasive species, and its presence may be responsible for a partial change in the structure of the native parasitoid fauna in the form of a decrease in their relative abundance. On the other hand, *L. testaceipes*, often, parasitizes populations of common and often even exotic pest species such as *Toxoptera aurantii* (Boyer de Fonscolombe) and *Aphis spiraecola* (Patch) (Žikic et al. 2015). In Algeria, L. testaceipes is considered promising as a naturalized biocontrol agent against the newly invasive pest in the Mediterranean; *Aphis illinoisensis* (Shimer) (Laamari et al. 2016).

The two species *Aphidius funebris* and *A. ervi* were also among the most abundant parasitoid species in the study area, with relatively a quite number of associations and host spectrums.

The parasitoid *Aphidius funebris* was the most dominant in the site of Fouhala than in the other two sites dominated by *A. matricariae* and *L. testaceipes*. It was reported on 7 species of aphids, but it showed a preference to parasitize the aphid species of the genus *Uroleucon*. The same remarks were mentioned by Talebi et al. (2009) and Aggoun et al. (2016).

*Aphidius ervi*, the parasitoid of alfalfa aphids, is a Palearctic oligophagous species associated mainly with Macrosiphin aphids, such as *Acyrthosiphon pisum* on legumes and, in a lesser measure, with * Macrosiphum euphorbiae* Thomas and *Aulacorthum solanii* (Kaltenbach) (Kos et al. 2009). In the present study, this species was reported by 10 associations, especially on *Uroleucon ambrosiae* and *U. sonchi* (Table 1). This oligophagous parasitoid is used as

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**Table 1** Tri-trophic associations, plant-aphid-parasitoid, noted at the oasis ecosystems in the region of Biskra between 2014 and 2016 (Continued)

| Parasitoids              | Parasitized aphid species | Host plant                  |
|-------------------------|---------------------------|-----------------------------|
| *Praon yomenae* (Takada, 1968) | *Uroleucon compositae* (Theobald) | *Onopordon macracanthum* |
|                         | *Uroleucon ambrosiae* (Thomas) mixed with *Hyperomyzus lactucae* (Linnaeus) | *Centaurea sp.* |
|                         | *Hyperomyzus lactucae* (Linnaeus) | *Taraxacum officinale* |
|                         | *Sonnchus oleraceus* | *Sonchus oleraceus* |

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a biological control agent for many species of aphids, especially against large aphid species (Kos et al. 2009).

The presence of parasitoid species with an intermediate number of associations and the host spectrum can be described as intermediate, such as the cases of Aphidius colemani, Diaeretiella rapae, L. fabarum, P. volucre, P. yomenae, and B. angelicae.

The species A. colemani was found associated much more with aphids of fruit trees (Aphis punicae and Hyalopterus pruni). It is also considered among the most dominant species on ornamental plants in the urban environment of Biskra (Hemidi et al. 2013), and in the oasis in the Ghardaïa region (Chehma and Laamari 2014).

In the Mediterranean basin, A. colemani was isolated from mummies of Melanaphis donacis (Passerini) and H. pruni in Morocco, Italy, and France (Stary and Sekkat 1987). It was also reported in Tunisia on H. pruni (Ben Halima and Ben Hamouda 2005) and on Aphis gossypii (Boukhris-Bouchachem 2011). In the Southern parts of Western Europe, this species is naturally absent (Laamari et al. 2012).

Diaeretiella rapae was found mainly associated with barley aphids, Rhopalosiphum maidis and Metopolophium dirhodum and on Myzus persicae infesting Lepidium draba (Brassicaceae) (Table 1). This association was also mentioned in other regions in Algeria (Chehma and Laamari 2014; Tahar Chaoche and Laamari 2015; and Laamari et al. 2016). Laamari et al. (2016) noted that this species was found at several locations in all cereal crops, and it was considered as the most important parasitoid of the Russian wheat aphid Diuraphis noxia (Kurdjumov).

An overall analysis of the data in the study area showed the habitat preferences of Lysiphlebus fabarum, as well as its specific activity on general aphids, belong to the genus Aphis. It parasitized the aphids that appeared on plant species belonging to 4 botanical families: Asteraceae, Fabaceae, Poaceae, and Amaranthaceae.

The Praon genus is represented in the present study by 2 species; P. volucre and P. yomenae. Those showed a preference for Macrosiphini aphids, especially Uroleucon species. The same results were found in other regions of Algeria by Laamari et al. (2011, 2012).

In general, species of the genus Binodoxys are specialized in parasitism of aphids found on herbaceous plants (Lazarević et al. 2017), but in the area of this study, the parasitoid Binodoxys angelicae was found associated with Aphis rumicis infesting Rumex sp. It was found to parasitize Aphis punicae installed on pomegranate.

Monophagous or specific parasitoid species attacking one or two aphid species are also present. That was found in cases of Aphelinus mali, Aphidius sonchi, Binodoxys sp, Ephedrus niger, and Lysiphlebus confusus.

The parasitoid Aphelinus mali emerged from a single host species of aphids, Hyperomyzus lactucae on Sonchus oleraceus. The presence of this parasitoid was noted only twice in Algeria: on Eriosoma lanigerum associated with Malus communis, in Northern and Eastern Algeria (Laamari et al. 2011; Aroun 2015).

The species Aphidius sonchi has been well developed on the aphidian species Capitophorus inulae associated with Dittrichia viscosa. It has been reported only once in Eastern Algeria on Hyperomyzus lactucae associated with Sonchus oleraceus (Laamari et al. 2012). In the present study, it was also collected from H. lactucae associated with Sonchus oleraceus.

Binodoxys sp, was recorded for the first time in Algeria parasitizing Hyadaphis foeniculi (Passerini) on Rubia tinctorum (Rubiaceae).

Ephedrus niger was reported only once in Algeria by Laamari et al. (2011) who collected it from Brachycoccus helichrysi on an ornamental plant Myoporum lae. In the present study, this species was collected only from the region of Branis, which represents the mountain oasis system from Capitophorus inulae Passerini and Ovatus inulae Walker, two specific aphids on the viscous Inula, Dittrichia viscosa (Asteraceae). The same behavior was found in the parasitoid, Lysiphlebus confusus, that found only on the Aphis fabae associated with Solanum nigrum in the same region.

An analysis of the tri-trophic associations constituted in the different oasis ecosystems of the Biskra region allowed to find out primordial results, which constitute a very important source of ecological information on the aphid parasitoids as biocontrol agents.

Given the number of associations formed during this study, it is noted that some parasitoids had a large dispersal capacity, in particular, the species belonging to the genera Aphidius and Lysiphlebus.

The parasitoids identified in the present study showed a specialization gradient, ranging from a group of species with a high degree of specialization (as in cases of Binodoxys sp, Ephedrus niger, and Lysiphlebus confusus) to a high degree of generalist (as in cases of A. mali, A. sonchi, and L. testaceipes) with many intermediate statuses. Some generalists’ parasitoid species showed a preference towards some host species (e.g., Aphidius funebris). Some aphid parasitoid species had preferences towards the habitat, the host plant, the botanical family, etc., all these parameters had an impact on the trophic associations formed. Generally, generalists were the most abundant. Navasse (2016) reported that the existence of generalist parasitoids is strongly questioned because with the dominance of specialists, there is a risk of limiting the possibilities of exchanges between cultivated and wild resources of agroecosystems. So, generalists may prove as an important resource for biological control programs in the future.

It has been, also, observed that the host (aphids) include both economic and non-economic species, and
some species of aphid parasitoids did attack both types of hosts, so these non-economic species may play a potential role as alternative hosts of parasitoid species in case of absence of their main hosts.

This study assessed the potential of non-crop areas as reservoirs for parasitoids available for crop protection.

Finally, the oasis ecosystems of this region have an appreciable richness of parasitoids than the other surveys carried out in the same region. This can be explained by the complexity and heterogeneity of these environments, which offer a favorable and relatively stable environment for the conservation of these natural enemies.

Conclusion
The study revealed a survey of certain aphid species with their specific parasitoids on certain host plants in the oasis ecosystems of the region of Biskra, Algeria. The tri-trophic associations showed a high potential of the surveyed parasitoid fauna in the region for biological control of aphids.

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Authors’ contributions
WH conduct the experiment, data collection and data analysis, drafted the manuscript. ML identified the host aphids. Both authors read and approved the final manuscript.

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Availability of data and materials
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Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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