

Multitrophic Interactions Between Coccinellids and Their Parasitoids in Natural and Managed Plant Systems: Host Plant and Aphid Prey Species Matter

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Abstract

Background: To better inform conservation biological control of aphids multitrophic interactions between aphids, coccinellids and their parasitoids in natural and managed plant systems were examined over 4 years.

Methods: Coccinellid larvae found naturally feeding on aphids on two non-crop plants growing in agricultural landscapes in Pakistan; *Aphis nerii* (Boyer de Fonscolombe) feeding on *Calotropis procera* L. and *Nerium oleander* L.; and four crop host; *Lipaphis erysimi* (Kalt) feeding on *Eurica sativa* Mill. and *Brassica campestris* L., *Uroleucon compositae* (Theobold) feeding on *Carthamus tinctorius* L., and *Diuraphis noxia* (Mordvilko) feeding on *Hordeum vulgare* L.; were collected throughout the aphid season and reared on their respective aphid-plant combination in the laboratory to identify coccinellid species, their parasitoids and performance (survival and pupal weight).

Results: Coccinellid pupal weight on different host plant-aphid combinations varied from 3.4 ± 1.8 to 11.2 ± 0.9 mg (mean \pm SE), as did mortality of coccinellid larvae due to diseases and unknown causes (5 ± 2.2 to $31 \pm 3.8\%$). Parasitism of coccinellid larvae by *Homalotylus flaminus* (Dalman) (Hymenoptera: Encyrtidae) ranged from ca 10 ± 2 to $30 \pm 3\%$ in *B. campestris* and *E. sativa*, respectively. Parasitism of coccinellid pupae by *Oomyzus scaposus* (Thomson) (Hymenoptera: Eulophidae) ranged between 17 ± 2.7 (*C. procera*) to $41 \pm 2.9\%$ (*B. compestris*). One *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) was reared.

Conclusions: Coccinellids were host plant and aphid selective. Some coccinellids were never or rarely recorded on a particular aphid-plant combination, suggesting that their prey selection more specific than often assumed. Management decision and conservation biological control cannot be based on superficial categories such as “aphids” and “coccinellids” but needs to be plant and species specific.

Background

Most predatory arthropods, including aphidophagous insects, are supposedly generalist predators that attack a variety of prey [1] but are often restricted to some degree in what they will eat [2]. Restricted use of prey may arise from low food availability [3] or reflect different prey specializations or even plant effects [4]. Similarly, the impact of parasitoids on their hosts may depend on the availability of alternate hosts [5], or plants that provide nectar and pollen for females [6]. Thus, aphids, other herbivorous insects, and plants may interact indirectly through shared natural enemies. Such interactions may be either negative (apparent competition) or positive (apparent mutualism), and may have important consequences for the herbivores' host plants [7] and management of pest species [8, 10].

Coccinellids are important natural enemies of whitefly, aphids, mealybugs, scales and mites in both natural and managed plant systems [11, 12]. They have been linked to biological control more than any

other group of predatory organisms and used in pest management programs for over a century [13]. They are often perceived as generalist predators [14, 15] and have been used in integrated pest management (IPM) and in augmentative biological control programs against various aphids since the 1950s [16, 17]. Conservation approaches, such as intercropping [18] and other modifications of agriculture practices, such as supplemental food sprays to attract and retain predators and parasitoids in crops [19, 20], provide ways to encourage coccinellids to enter managed ecosystems and increase their effect on aphid populations [21, 22]. The widespread planting of transgenic crop varieties has reduced insecticide use against lepidopterous pests [23]. Incidental control of non-lepidopterous pests has consequently declined and the importance of Coccinellidae, and landscape elements that may act as refuges for them [24], in IPM for aphid pests of crops has increased [20].

Coccinellids are also attacked by a variety of natural enemies [25], although few of these are thought to significantly alter their population dynamics [26]. Coccinellids are attacked in all life stages with nearly 100 species of parasitoids recorded in the Hymenoptera and Diptera [25]. Few parasitoids of entomophagous coccinellids are specialists, some are widely distributed and attack within a subfamily or tribe. One of the best understood parasitoids is *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae), whose host preference, life history, ecology, and behavior have been thoroughly investigated [27, 28]. Adult coccinellids were preferred hosts, especially older females [29, 30], but immature parasitoids have been found in host larvae and pupae [31]. As a solitary endoparasitoid of adults, *D. coccinellae* prefers larger species of Coccinellinae [25]. Coccinellids vary in their suitability as hosts for *D. coccinellae* [32], but the mechanisms that influence realized rates of parasitism of various species are unknown. Comparing primary and secondary parasitism rates suggests that at least some coccinellids are able to overcome parasitoid larvae [33]. Parasitization of coccinellids can lead to a considerable decrease in their populations prior to hibernation, possibly reducing the future effect of these predators against spring outbreaks of aphids [34]. Most reports of coccinellid parasitoids are simple host records with no data on the impact of these natural enemies on population dynamics of their hosts [35].

Here we examine the trophic interactions between various species of prey aphids, their ladybeetle predators and the parasitoids of the lady beetles in managed and natural plant systems. The objectives of this study were to determine the diversity of ladybeetle species in managed and natural plant systems, evaluate coccinellid development and survival on the various aphid-host plant combinations and to record parasitoids of the immature coccinellids in larval and pupal stages. This work will help lay the basis for better management of agricultural systems to improve management of aphid pests.

Methods

Insect collection and rearing

Larvae of coccinellid species feeding upon aphids on various plants were collected from the field and reared in the laboratory on their respective plant-aphid combination. We sampled from two types of plant systems, a disturbed agroecosystem, and an undisturbed or natural plant system in various years

(Table 1). Experiments and observations on collected material were conducted under laboratory conditions at the Department of Entomology, Sindh Agriculture University Tandojam, Pakistan. Each week ladybeetle larvae were collected from each host plant-aphid combination growing on the University Campus grounds and nearby experimental fields. The beetle larvae collected from different plant-aphid combinations were divided at random into four groups (designated as replicates) and reared on their respective host plants and aphids in plastic jars (30 × 20 cm) until adult beetle emergence or emergence of parasitoids from larvae or pupae. Collection and rearing started with the appearance of aphids and their coccinellid predators in the field. Sampling and collection of larvae continued until crops matured and were harvested, or the disappearance of aphids and their coccinellid predators from plants due to high temperatures at the onset of summer. The six host plants and their associated aphid species (Table 1) included four plants grown as cultivated crops and two non-crop plants: calotropis is a widespread weed growing on uncultivated lands and channel embankments and oleander is garden and roadside ornamental.

Table 1
Host plant-aphid-coccinellid beetle systems collected during 2010, 2011, 2013 and 2014 at Tandojam, Pakistan

No.	Host plant	Aphid species	Associated coccinellids
1	Mustard <i>Brassica campestris</i> L. (Brassicaceae)	<i>Lipaphis erysimi</i> (Kaltenbach)	<i>Coccinella septempunctata</i> L., <i>Coccinella undecimpunctata</i> L., <i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.
2	Rocket <i>Eurica sativa</i> L. (Brassicaceae)	<i>Lipaphis erysimi</i> (Kaltenbach)	<i>Coccinella septempunctata</i> L., <i>Coccinella undecimpunctata</i> L., <i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.
3	Safflower <i>Carthamus tinctorius</i> L. (Asteraceae)	<i>Uroleucon compositae</i> (Theobold)	<i>Coccinella septempunctata</i> L., <i>Coccinella undecimpunctata</i> L., <i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.
4	Barley <i>Hordeum vulgare</i> L. (Poaceae)	<i>Diuraphis noxia</i> (Mordvilko)	<i>Coccinella septempunctata</i> L., <i>Coccinella undecimpunctata</i> L., <i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.
5	Calotropis <i>Calotropis procera</i> L. (Apocynaceae)	<i>Aphis nerii</i> (Boyer'de Fonscolonde)	<i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.
6	Oleander <i>Nerium oleander</i> L. (Apocynaceae)	<i>Aphis nerii</i> (Boyer'de Fonscolonde)	<i>Minochilus sexmaculatus</i> F. and <i>Brumus suturalis</i> F.

The coccinellid larvae were provided with fresh food daily until they pupated. Final instar fully-grown larvae and pupae were kept individually in labelled plastic vials (70 × 30 mm) and checked twice daily to determine when parasitoids emerged or adult ladybeetles eclosed. After emergence, the parasitoids were preserved in 70% alcohol, labeled and sent to CABI Bioscience, Central and West Asia, Rawalpindi, Pakistan for identification. Weights of coccinellid pupae and adult beetles were recorded on a balance ((Ohaus®, Galaxy 160) one day after pupation and eclosion respectively. Coccinellids could only be identified to species with certainty after adult eclosion, so records of parasitoids from immatures could only be associated with host plant and aphid species.

STATISTICAL ANALYSIS

After adult eclosion, the effect of different plant-aphid combinations on coccinellid species diversity was determined by analysis of variance (ANOVA). Before ANOVA, data were square root transferred ($\sqrt{x+0.5}$) to stabilize variance [65]. The mean mortality of coccinellid beetles collected on different host plants caused by different factors was compared by ANOVA. The mean number of larval and pupal parasitoids emerging from each larva/ pupa and pupal weight of coccinellid beetles were tested by ANOVA performed separately for the 2010 and 2011 and 2013 and 2014, because of different plant-aphid systems sampled. Regression analyses were carried out to ascertain effect of host plant on relationship between pupal weight and number of parasitoids emerging from each pupa. All the data were analyzed using statistical software (STATISTIX® VERSION-8.1, Analytical Software, Inc. Tallahassee, FL. USA).

Results

Coccinellid species associated with different host-aphid plant combination

Four coccinellid species were recorded in this study. Only *Menochilus sexmaculatus* Fab and *Brumus suturalis* Fab were recorded on calotropis and oleander and the number of *M. sexmaculatus* was significantly greater on these plants (calotropis: $F_{3,21}=89.98$, $P = 0.0001$; 2010 and 2011) (oleander: $F_{3,21}=137.84$, $P = 0.0001$; 2013 and 2014) compared to other systems. The numbers of *Coccinella septempunctata* L. were significantly higher than those of other ladybeetles on mustard ($F_{3,21}=44.21$, $P = 0.0001$; 2010 and 2011). Safflower significantly affected the the number sof different species of coccinellids recorded ($F_{3,21}=24.22$, $P = 0.0001$; 2010 and 2011) and the highest numbers of *C. undecimpunctata* L. were recorded on this plant. There were significant differences in abundance among species on barley ($F_{3,21}= 11.89$, $P = 0.0001$; 2010 and 2011), with *B. suturalis* most abundant on this host. The numbers of *C. septempunctata* were significantly higher on rocket than on other host plants ($F_{3,21}=3.71$, $P = 0.027$; 2013 and 2014). The populations of all coccinellid predators were significantly higher during 2010 compared with 2011 which may be due to differences in climatic conditions.

Records Of Larval Mortality

The mortality of ladybird beetle larvae collected from different host plants due to diseases and unknown causes did not vary significantly within years ($F_{3,33} = 0.48$, $P = 0.7005$, 2010; $F_{3,9} = 0.87$, $P = 0.49$, 2011; $F_{2,6} = 0.09$, $P = 0.9155$, 2013, and $F_{2,6} = 0.12$, $P = 0.8847$, 2014) and ranged between 5 ± 2.2 and $31 \pm 3.8\%$ (mean \pm SE). However, mortality varied significantly among years (Table 2). The lowest and the highest coccinellid larval mortality were recorded on barley and calotropis plants, respectively (Table 2). Coccinellid larval mortality caused by the gregarious larval parasitoid, *Homalotylus flaminus* Dalman (Hymenoptera: Encyrtidae), on different host plant-aphid combinations was not significantly different within years ($F_{3,33} = 0.48$, $P = 0.689$, 2010; $F_{3,9} = 0.06$, $P = 0.978$, 2011; $F_{2,6} = 3.27$, $P = 0.1097$, 2013; $F_{2,6} = 1.08$, $P = 0.399$, 2014) and ranged from 9.6 ± 1.98 to $36.3 \pm 2.7\%$ in larvae collected from mustard and safflower, respectively. The number of adult parasitoids emerging from single host larvae collected from different host plants varied significantly ($F_{3,72} = 12.9$, $P = 0.0001$, 2010; $F_{3,56} = 15.7$, $P = 0.0001$, 2011; $F_{2,32} = 5.59$, $P = 0.0083$, 2013; $F_{2,34} = 10.73$, $P = 0.0002$, 2014) and ranged from 2.2 ± 0.11 on oleander to 7.1 ± 0 on safflower (Table 3).

Table 2

Percent mortality (Mean \pm SE) of entomophagous coccinellids collected from different plant systems during 2010, 2011, 2013 and 2014 and reared on aphids feeding on *Calotropis procera*, *Brassica campestris*, *Carthamus tinctorius*, *Hordeum vulgare*, *Eurica sativa*, and *Nerium oleander* due to natural (& unknown) causes, and larval and pupal mortality due to parasitoids. The SE are calculated over time (collections)

Host plant	Natural mortality	Larval mortality	Pupal mortality	Total (n)
2010				
<i>Calotropis procera</i> & <i>Aphis nerii</i>	7.5 \pm 2.5	13.8 \pm 5.0ab	25.4 \pm 11.3	46.7 (240)
<i>Brassica campestris</i> & <i>Lipaphis erysimi</i>	6.2 \pm 2.5	9.6 \pm 2.0b	30.0 \pm 11.9	45.8 (240)
<i>Carthamus tinctorius</i> & <i>Uroleucon compositae</i>	6.3 \pm 1.3	15.8 \pm 8.9ab	28.3 \pm 10.1	50.4 (240)
<i>Hordeum vulgare</i> & <i>Diuraphis noxia</i>	5.0 \pm 2.16 ns	17.1 \pm 10.8a	27.1 \pm 15.0 ns	49.1(240)
2011				
<i>Calotropis procera</i> & <i>Aphis nerii</i>	36.3 \pm 2.7	22.5 \pm 2.1	31.3 \pm 2.5	90.1 (80)
<i>Brassica campestris</i> & <i>Lipaphis erysimi</i>	41.25 \pm 2.9	23.8 \pm 2.2	27.5 \pm 2.3	92.5 (80)
<i>Carthamus tinctorius</i> & <i>Uroleucon compositae</i>	33.8 \pm 2.6	23.8 \pm 2.2	36.3 \pm 2.7	93.9 (80)
<i>Hordeum vulgare</i> & <i>Diuraphis noxia</i>	31.2 \pm 2.5 ns	25.0 \pm 2.2 ns	32.5 \pm 2.5 ns	88.7 (80)
2013				
<i>Calotropis procera</i> & <i>Aphis nerii</i>	21.3 \pm 2.9	21.3 \pm 2.9	16.8 \pm 2.7b	59.4 (160)
<i>Nerium oleander</i> & <i>Aphis nerii</i>	21.3 \pm 3.2 ns	21.3 \pm 8.8 ns	24.4 \pm 2.7a	67 (160)
<i>Eurica sativa</i> & <i>Lipaphis erysimi</i>	20.0 \pm 2.7	23.8 \pm 3.0	21.9 \pm 2.8ab	71.9 (160)
2014				
<i>Calotropis procera</i> & <i>Aphis nerii</i>	31.3 \pm 3.8	20.0 \pm 3.5	23.8 \pm 2.4	75.1 (80)
<i>Nerium oleander</i> & <i>Aphis nerii</i>	25.0 \pm 3.5 ns	16.3 \pm 3.2 ns	22.5 \pm 4.0 ns	63.8 (80)
<i>Eurica sativa</i> & <i>Lipaphis erysimi</i>	26.3 \pm 5.5	22.5 \pm 4.3	23.8 \pm 5.5	72.6 (80)
Means \pm SE followed by same letter in a vertical column are not significantly (P < 0.05) different from each other by LSD test. ns = non-significant. The ANOVA for each year was done separately.				

Table 3

Summary of larval and pupal parasitoid load and pupal weight of entomophagous coccinellids collected from different plant systems during 2010, 2011, 2013 and 2014.

Treatments	Year	No: of Larval parasitoids/Larva	Pupal weight(mg)	No: of Pupal parasitoids/Pupa
Calotropis	2010	3.3 ± 0.1c	6.1 ± 5.7c	11.5 ± 1.2c
<i>(Calotropis procera)</i>	2011	4.1 ± 0.1c	5.1 ± 0.1d	7.61 ± 0.4d
	2013	3.3 ± 0.5ab	2.9 ± 01.9b	8.4 ± 9.0b
	2014	3.6 ± 0.1b	4.9 ± 1.8b	17.8 ± 0.5b
Oleander	2013	2.5 ± 0.8b	5.2 ± 1.8c	18.5 ± 5.9a
<i>(Nerium oleander)</i>	2014	3.3 ± 0.4c	3.4 ± 1.2c	12.4 ± 0.4c
Mustard	2010	4.3 ± 0.1a	9.15 ± 0.7b	23.0 ± 0.2b
<i>(Brassica campestris)</i>	2011	5.7 ± 0.4b	7.6 ± 0.1b	18.3 ± 0.7b
Rocket	2013	4.1 ± 0.7a	3.7 ± 1.8b	10.4 ± 1.2b
<i>(Eurica sativa)</i>	2014	3.9 ± 0.4a	7.2 ± .8a	30.8 ± 0.6a
Safflower	2010	3.9 ± 0.1b	11.2 ± 0.9a	29 ± 2.1a
<i>(Carthamus tinctorius)</i>	2011	7.3 ± 0.8a	8.4 ± 0.1a	27.8 ± 0.7a
Barley	2010	3.3 ± 0.1c	6.8 ± 0.3c	13.9 ± 1.1c
<i>(Hordeum vulgare)</i>	2011	3.8 ± 0.5c	5.6 ± 0.2c	10.7 ± 0.5c
Means ± SE followed by same letter in a vertical column are not significantly ($P < 0.05$) different from each other by LSD test. The ANOVA for each year was done separately.				

Coccinellid Pupal Weights

The weight of coccinellid pupae reared on different host plant-aphid combinations varied significantly ($F_{3, 125}=15.9$, $P = 0.0001$, 2010; $F_{3, 72}=12.9$, $P = 0.0001$, 2011; $F_{2, 108}=15.38$, $P = 0.0001$, 2013; and $F_{2, 36}=25.31$, $P = 0.0001$ 2014) and ranged from 2.9 ± 01.91 on calotropis to 11.20 ± 0.90 mg on safflower. Mortality caused by the gregarious pupal parasitoid, *Oomyzus scaposus* (Thomson) (Hymenoptera: Eulophidae), on different host plants did not differ significantly within years ($F_{3, 33}=1.82$, $P = 0.698$, 2010; $F_{3, 9}= 0.65$, $P = 0.601$ 2011; $F_{2, 6}=4.67$, $P = 0.0599$, 2013; $F_{2, 6}=0.04$, $P = 0.963$, 2014) and ranged between 16.8 ± 2.7 on calotropis to $41.3 \pm 2.9\%$ on mustard. The number of adult *O. scaposus* emerging from each pupa varied significantly ($F_{3, 125}=26.4$, $P = 0.0001$, 2010; $F_{3, 100}=247.0$, $P = 0.0001$, 2011; $F_{2, 108}=23.5$ $P = 0.0001$, 2013; $F_{2, 36}=18.78$, $P = 0.0001$, 2014) and ranged from 7.6 ± 0.4 parasitoids per pupa on calotropis to 30.8 ± 0.6

on rocket. The relationship between pupal weight and number of parasitoids per coccinellid pupa was significant in most cases and larger pupae typically supported more parasitoids than smaller pupae (Table 4). In 2010, a single *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) was reared from a coccinellid collected on safflower.

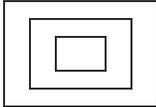
Table 4

Linear regression equations of coccinellid pupal weight (x) and number of parasitoids/ pupa (Y) for *Calotropis procera*, *Brassica campestris*, *Carthamus tinctorius*, *Hordeum vulgare*, *Eurica sativa*, and *Nerium oleander* when used as host plant of *Aphis nerii*, *Lipaphis erysimi*, *Uroleucon compositae* and *Diuraphis noxia*. All regressions are significant (at $P < 0.05$) except for *C. procera* in 2014.

Relation between pupal weight and No. of parasitoids per pupa		Linear regression equations	Determination coefficients
<i>Calotropis procera</i>	2010	$Y = 4.3273x - 14.417$	$R^2 = 0.7713$
	2011	$y = 2.3098x - 4.0581$	$R^2 = 0.8714$
	2013	$y = 2.5776x - 5.4522$	$R^2 = 0.8102$
	2014	$y = -0.0351x + 18.193$	$R^2 = 0.0005$
<i>Brassica campestris</i>	2010	$y = 2.2059x + 4.8161$	$R^2 = 0.7486$
	2011	$y = 4.8663x - 18.711$	$R^2 = 0.8501$
<i>Carthamus tinctorius</i>	2010	$y = 3.8717x - 12.356$	$R^2 = 0.8474$
	2011	$y = 4.589x - 10.805$	$R^2 = 0.7587$
<i>Hordeum vulgare</i>	2010	$y = 3.8717x - 12.356$	$R^2 = 0.8474$
	2011	$y = 2.8692x - 5.4169$	$R^2 = 0.7926$
<i>Eurica sativa</i>	2013	$y = 4.3863x - 5.3811$	$R^2 = 0.7904$
	2014	$y = 5.2347x - 7.1736$	$R^2 = 0.5927$
<i>Nerium oleander</i>	2013	$y = 4.9366x - 5.3362$	$R^2 = 0.7486$
	2014	$y = 3.1201x + 1.9747$	$R^2 = 0.8736$

Table 5
Influence of host plant- prey combination on adult weight (mg) of coccinellids

Coccinellids	<i>Brassica campestris</i>	<i>Eurica sativa</i>	<i>Hordeum vulgare</i>	<i>Nerium oleander</i>	<i>Calotropis procera</i>
<i>Menochilus sexmaculatus</i> F.	11.0 ± 0.5c	9.9 ± 0.8c	7.5 ± 0.6d	18.4 ± 0.7a	14.7 ± 0.4b
<i>Coccinella septempunctata</i> L.	27.1 ± 0.7a	21.2 ± 0.8b	19.9 ± 1.0b		
<i>Coccinella undecimpunctata</i> L.	32.4 ± 1.0a	24.9 ± 0.5b	26.2 ± 1.5b		
<i>Brumus suturais</i> F.	5.0 ± 0.5a		4.2 ± 0.3a		



Means ± SE followed by same letter in horizontal rows are not significantly ($P < 0.05$) different from each other by LSD test.

Coccinellid Adult Weights

Significant differences in adult weights were recorded, depending on the host plant-aphid combination. At eclosion, *M. sexmaculatus* adults fed with aphids from *Nerium oleander* were significantly ($F_{4,45}=43.8$, $P = 0.0001$) larger than those fed with aphids from other host plants. *Cocinella septempunctata* adults fed on aphids from *Brassica campestris* were significantly ($F_{2,27}= 19.5$, $P = 0.0001$) heavier than other host plant-aphid combinations. Adults of *C. undecimpunctata* reared on *B. campestris* were significantly ($F_{2,27}=9.04$, $P = 0.001$) larger than adults reared on other aphid-host plant combinations. There was no significant ($F_{1,18}=2.19$, $P = 0.1565$) difference in adult weight of *B. suturalis* fed with aphids reared on either *B. campestris* or *H. vulgare*.

Discussion

Greater numbers of larval and pupal parasitoids emerged from coccinellid larvae and pupae collected from crop plant hosts than non-crop plant hosts. The higher number of larval and pupal parasitoids emerging from a single larva and pupa, and higher pupal weight supporting more parasitoids from crop plants compared with non- crop plants, may have a negative impact on development of coccinellid populations in crop ecosystems and the biological control of insect pests. Coccinellids are important natural enemies of phytophagous insects in natural and managed ecosystems [42] and play a significant role in biological control of pest insects in agroecosystem [12, 22]. There was a significant relationship between the number of parasitoids emerging per pupa and pupal weight of hosts. Higher resource

availability for a developing parasitoid is assumed in larger hosts [35, 36]. Better parasitoid survival, larger body size, increased longevity and higher fecundity rates are expected with greater resource availability than for parasitoids emerging from low quality hosts [37]. The increased parasitization of predatory coccinellids may have negative impact on IPM of phytophagous insects in agriculture settings.

Host plant influences the nutritional quality of aphid prey for predatory coccinellids [38, 42]. The positive (nutritive) and negative (toxic) trophic effects are manifested in the biological performance of predators. In the present study significant variation was found in pupal and adult weight of coccinellids feeding on different host plant-aphid prey combinations. [39] reported that the adult weight of *Adalia bipunctata* L. depended on the host plant of the prey and adults of *A. bipunctata* fed with aphids from *S. alba*. and *B. napus* were larger than those fed with *M. persicae* reared on *V. fabia*. [43] found significant host plant-aphid effects for adult mass at emergence. The suitability of each aphid species was improved by rearing on its host plant of origin and diminished by rearing on alternative host plants. [44], observed that prey species significantly affected adult weights of *Hippodamia convergens* Guérin-Ménéville, surviving adults weighed less when provided with Brassica-specialist aphids, *L. erysimi* or *Brevicoryne brassicae* (L.), than when fed the generalist *M. persicae*. The specialist aphids sequestered high levels of indole glucosinolates from their host plants that were toxic to aphid predators.

Several species of hymenopteran parasitoids parasitize different life stages of coccinellid beetles in various regions [25]. The most important among them are *D. coccinellae*, several species of *Homalotylus* and *O. scaposus* [45]. In the present study, three parasitoid species were recorded on coccinellid beetles, two gregarious species (*H. flaminus* on larvae (10–36% parasitism rate) and *O. scaposus* (17–42% parasitism rate) and a solitary species (*D. coccinellae*) which was very rare (a single individual recorded from a coccinellid on safflower). *Dinocampus coccinellae* is typically found in cooler regions [46, 47] and is not prevalent in the comparatively hot climatic conditions of present study area.

Herbivorous insects are conventionally grouped into categories based on their degree of dietary specialization. Specialist herbivores have physiological adaptations to cope with the plant defenses, which allow greater tolerance of secondary plant substances produced by plants to defend against herbivory than most generalists [48]. There are natural enemies which are adapted to consuming toxic prey. Feeding by herbivores induces volatile organic compound (semiochemicals) emissions from host plants which help natural enemies locate and recognize their host or prey [49]. [50] investigated the electrophysiological and behavioral responses of the ladybird parasitoid *Dinocampus coccinellae* to the alkaloid precoccinelline of *C. septempunctata*, which is thought to provide a toxic defence for the ladybird.

Brassica plants are important vegetable and oil seed crops of agroecosystem and produce glucosinolates as defense against herbivory. The phytophagous insects and their predators have evolved mechanisms to cope with these compounds. The brassica specialist, *B. brassicae* sequesters glucosinolates as a defense against predators. Glucosinolates have been shown to affect performance of coccinellid predators in a concentration (dose)-dependent manner [51] and in this study adult weight of *C. septempunctata* and *C.*

undecimpunctata was significantly lower when these predators fed on *L. erysimi* collected from rocket rather than mustard.

The toxicity of milkweeds comes from bitter-tasting steroids glycosides (cardenolides) that have toxic effects on most animals. Cardenolides bind to the Na, K-ATPase pump making them a vertebrate toxin that functions in a dose-dependent manner and their production is known to be induced following damage by several species of herbivores [52, 53]. *Aphis nerii* feed in the cardenolide-rich internal phloem of host bicollateral vascular bundles [54], and these chemicals are present in *A. nerii* honeydew and body tissue [55, 56]. This aphid is found wherever milkweeds and oleander occur and it is known to sequester cardenolides, and use them as a chemical defense against a range of non-adapted natural enemies [57, 60]. Cardenolides are toxic to many coccinellids, including *C. septempunctata* [12] and *Adonia variegata* [58]. *Aphis nerii* is not toxic to *M. sexmaculata* [45]. In our study adult weight of *M. sexmaculata* feeding on *A. nerii* was significantly higher from oleander and calotropis as host plants compared with other aphid-host plant combination. [61] studied host preference of *M. sexmaculata* on five aphid species and found it developed best on *A. nerii*; see also [62]. Some generalist natural enemies of cardenolide-containing insects are deterred by the compounds [63]. In the present study, coccinellid larvae consuming *A. nerii* as a prey supported the lowest number of *H. flaminus* adults per larva compared with other prey species feeding on non-toxic host plants. Pupal weight of coccinellids was significantly less for coccinellids reared from calotropis and oleander compared with other host plants. Similarly, the number of adult parasitoids emerging from single coccinellid pupa was lowest when feeding on *A. nerii* on calotropis and oleander. Similarly, for parasitoids emerging from coccinellids pupae feeding on *A. nerii* compared with other host plants. This suggests that cardenolides negatively affected the fourth trophic level. *C. septempunctata* and *C. undecimpunctata* were not collected from calotropis and oleander plants indicating that these coccinellids are not adapted to feed on *A. nerii* and this aphid is toxic to them [64].

Conclusion

Coccinellids are important natural enemies of aphids, scale insects and other soft bodied insects infesting natural and managed plant systems. Coccinellid predators frequently move between crop and non-crop habitats that act as reservoirs, and provide biological control of aphid pests in agriculture habitats. Growing flowering plants around border rows of crops will encourage and attract coccinellid predators to colonize and to multiply and control aphid pests in crop habitats. The suppression of aphid populations by coccinellid predators provides environmental and economic benefits and may reduce yield loss without the negative environmental impacts of toxic pesticide use, but as we have found not all coccinellids feed equally as well on all aphids -host plant combinations. Designing better agricultural landscapes needs to take this into consideration.

Declarations

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Author's contribution

All authors contributed equally in order to conduct and prepare this manuscript.

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Figures

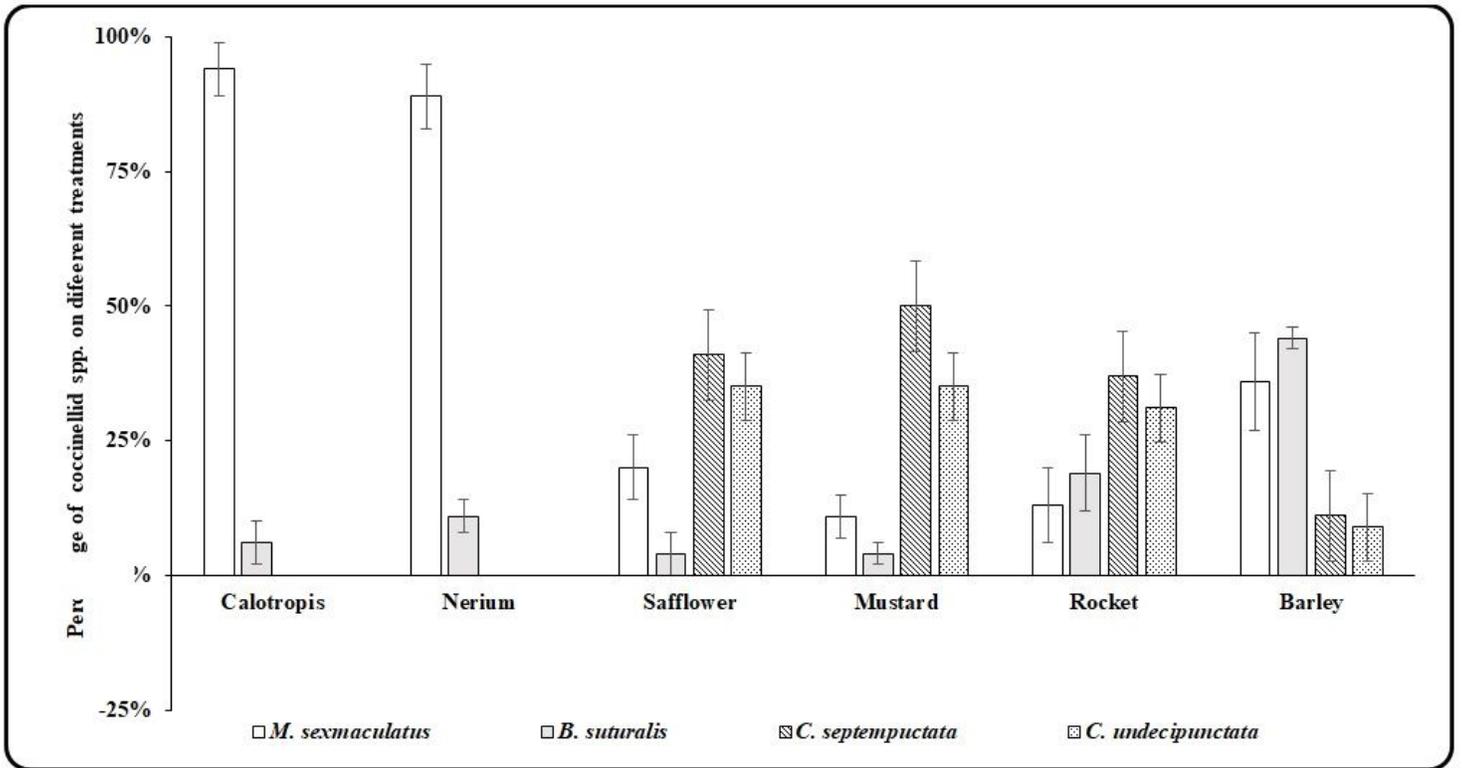


Figure 1

Means \pm SE relative abundance and diversity of coccinellid species on different host plants during 2010, 2011, 2013 and 2014.

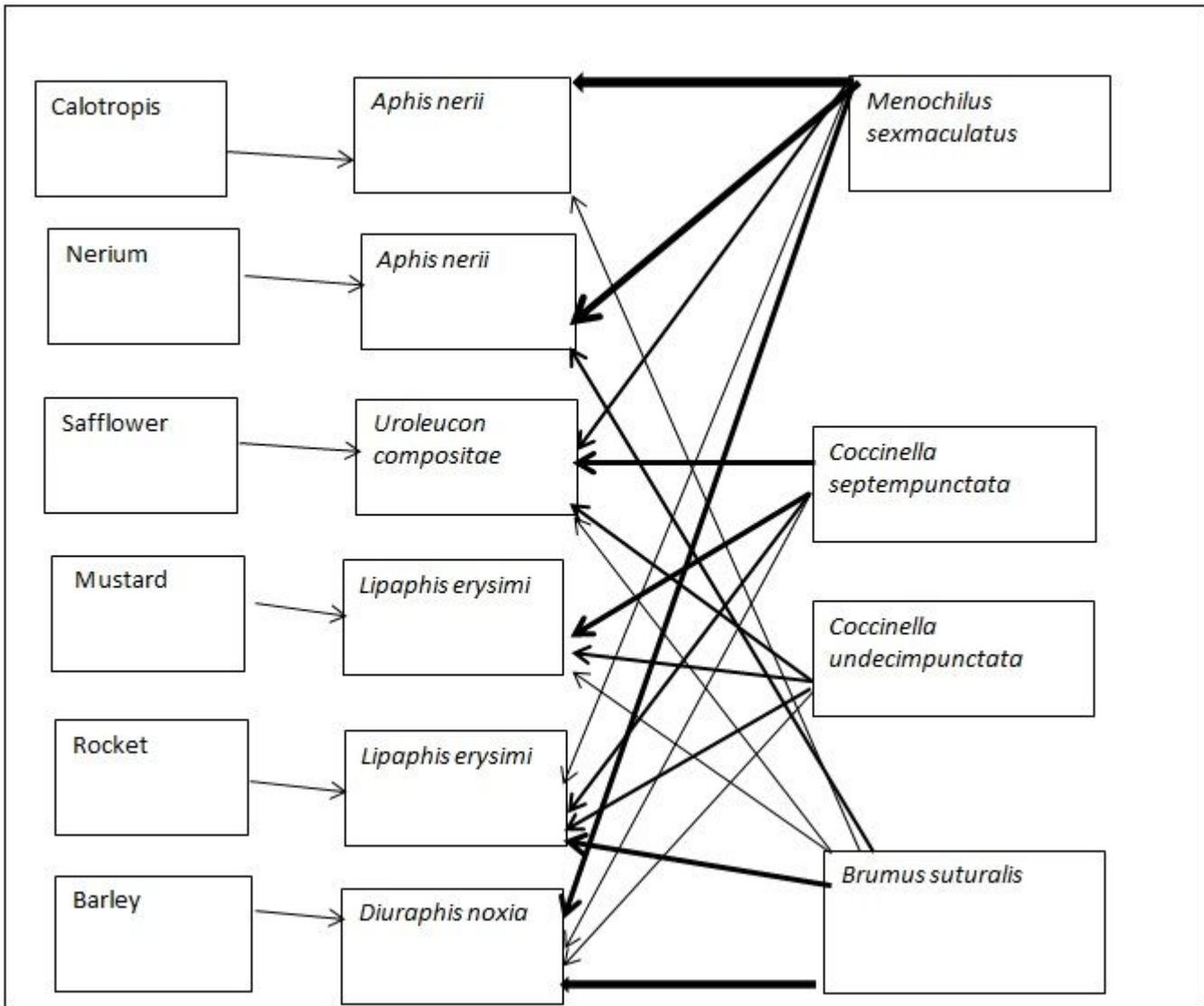


Figure 2

Interactions between host plants, aphid species and coccinellids under natural and managed plant systems. The arrows are proportional to how often different coccinellids are reared from each aphid-plant system.