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Parasitism of a leafminer in managed versus natural habitats

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Abstract

Parasitic assemblages of *Liriomyza huidobrensis* were analysed in relation to natural, urban and cultivated habitats through experimental and comparative methodologies. The field experiment consisted in placing potted plants previously mined in the laboratory in four localities representative of each habitat type for seven days, whereas naturally mined *Arctium minus* leaves were collected over several years in localities representative of different environments.

Results showed that overall parasitism and parasitoid species richness were not lower in simple and disturbed than in complex habitats. Pooled data indicated that parasitism of *L. huidobrensis* increased in the sequence natural < urban < cultivated on both experimentally exposed and naturally occurring weeds. Small leafminer populations attracted the highest total number of parasitoid species in cultivated habitats. Some degree of habitat specialisation was detected in eulophid species which were particularly scarce in cultivated habitats, the reverse being found for braconids.

Keywords: *Liriomyza huidobrensis*; Natural, urban and cultivated habitats; Parasitoid communities

1. Introduction

Ecological theory predicts that herbivores should exhibit greater species richness in natural than in cultivated habitats, a prediction that may be extended to higher trophic levels (Gurr et al., 1998). Parasitic Hymenoptera have the potential to control insect herbivore populations (La Salle and Gauld, 1993; Hawkins and Sheehan, 1994), but may be affected by habitat fragmentation and isolation (Tscharntke and Kruess, 1999; Kruess, 2003), and could hence constitute a good indicator of environmental disturbance (Matlock and de la Cruz, 2002).

Comparing arthropod diversity and abundance in managed crop systems and natural or feral systems could aid in developing effective control of pests (Gardiner et al., 2003). This paper examines the parasitic complex of a leafminer comprising endophagous species which are likely to reflect environmental changes because they are relatively host-specific (Cornell, 1989). *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) is a polyphagous leafminer, first described in Argentina, native to the Neotropics and currently recorded in many parts of the world as a pest on several ornamental, horticultural

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and cultivated plant species (Weintraub and Horowitz, 1995). *L. huidobrensis* occurs in several habitat types in the study area, but is particularly abundant on horticultural crops (Valladares et al., 1996, 1999). This leafminer sustains a large parasitic community, composed of eulophids, pteromalids, braconids and eucoilids (Salvo and Valladares, 1998, 1999; Valladares and Salvo, 1999) causing parasitism rates of 40% on average (Valladares et al., 2001).

The aim of the present study was to analyse the effect of habitat type on the parasitic assemblage of *L. huidobrensis* and to test the hypothesis that different host-parasitoid relationships exist among habitats in terms of number of host-parasitoid interactions, extent of parasitism and structure of parasitoid communities.

2. Methods

Parasitic assemblages of *L. huidobrensis* were analysed in relation to natural, urban and cultivated habitats through experimental and comparative methodologies. Habitats situated at least 10 km from big cities and dominated by non-cultivated vegetation were considered as ‘‘natural’’. Continuously disturbed landscapes dominated by buildings, roads and pavements, as ‘‘urban’’, and patches over 1000 m^2 cultivated for commercial purposes as ‘‘cultivated’’.

For experiments, field collected *L. huidobrensis* adults were offered broad beans (*Vicia faba* L.) and pumpkins (*Cucurbita maxima* Duch) in the laboratory. Pots (28 cm × 15 cm, 9 cm deep) containing 8–10 broad beans (6–10 leaves each) or four to six pumpkins (2–4 leaves each), were placed in a cage (glass, wood and voile, 30 cm side length) with 20 pairs for 4 h, at room temperature, for mating and oviposition. This procedure occurred simultaneously in four cages for each plant species, to obtain plants with a similar number of larvae per leaf. Five days later the pots with mined plants were taken to a given locality and placed 10 m from each other in the field. Seven days later the pots were brought back to the laboratory for rearing.

Replicates for habitat comparisons consisted of four localities per habitat type (five for pumpkins, which was repeated twice in one cultivated locality). Eight circles of 500 m diameter (19.6 ha) centred on experimental sites were visually analysed through photo-interpretation of a Landsat 5TM satellite image (bands: 7-5-2; spatial resolution: 30 m). The complete area of the circles chosen as urban and natural habitats were clearly homogeneous and typified as the corresponding habitat whereas in those circles selected for cultivated habitats a fraction of urbanization ranging from 0 to 10% was allowed. Natural localities were chosen as similar as possible, in terms of percentage of natural and introduced vegetation, proximity to rivers, altitude, etc. Four home gardens in Córdoba (capital of the province, two million inhabitants), at least 2 km apart from each other, were chosen as replicates for urban habitats. Representative localities of cultivated habitats consisted of four diversified (three to six cultivated plant species) horticultural and ornamental crop fields of small dimensions (1–3 ha) located on the outskirts of Córdoba. Natural vegetation in the field margins comprised between 2 and 5% of the total area of the fields. Conventional horticultural practices were used, applying a variable amount of synthesised pesticides (mainly dimetoate and cypermetrine, 2–5 applications per crop cycle) and artificial fertilisers (urea and diamonic phosphate, 150–250 kg/ha) (Tártara et al., 1998; Avila, personal communication). In these sites, pots were placed at the field margins. All replicates were carried out during November and December 1999 and 2000 for pumpkin, and 2000 and 2001 for broad bean.

Mined leaves of the weed *Arctium minus* (Hill) Bernh. were collected (1993–2000) under different habitats for laboratory rearing. Data collected at each locality were considered as replicates.

Data per replicate were summed up for the four pots or using all collections of *A. minus* in terms of: (1) number of parasitoid species; (2) number of species per family; (3) rate of parasitism. Parasitoid species richness and abundance of the dominant parasitoid species obtained from all replicates of the same habitat were pooled for analysis using the Chi-square test to detect dependence among habitat and the above-mentioned variables.

Data from field experiments were analysed through a nested ANOVA model with habitat (three levels) as a factor nested under year of replication (two levels). Larval density provided by each level of treatment was assessed by nested ANOVA. The effect of habitat type on species richness of parasitic complexes obtained from weed leaves was analysed through ANCOVA, including the total number of adults collected (log) as covariable. Parasitism rates were analysed by one-way ANOVA. Species richness values were log transformed and rates of parasitism were angularly transformed in all cases. Discriminant analysis (DA) was used to analyse the influence of habitat on parasitoid community composition. Parasitoid species abundance, expressed as the maximum value recorded for each host, was considered as the dependent variable. Data obtained from exposure experiments were analysed by pooling replicates of both plant species to examine the discriminatory power of year of sampling, host plant and habitat type, on the specific composition of the parasitic community. The same analysis was performed using data from naturally occurring weeds.

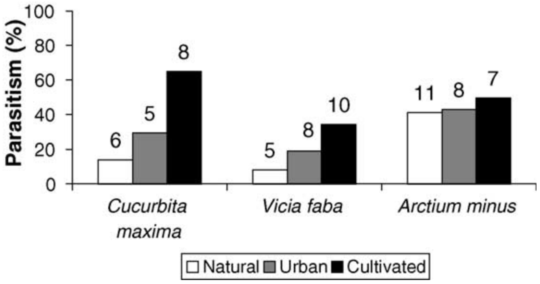

Fig. 1. Total parasitism of *Liriomyza huidobrensis* in natural (□), urban (▨) and cultivated (■) habitats and total number of parasitoid species.

3. Results

A total of 9272 adults (flies and parasitoids) were obtained, 7592 of which from plants in field experiments. Of the total, 22% were parasitoids, with 17 species from four families and six host-parasitoid associations recorded for the first time on *C. maxima* (Table 1). Nine parasitoid species represented less than 1% of the total number of individuals.

The richest complex and the highest parasitism rates of *L. huidobrensis* were recorded for cultivated habitats on both host plants (Table 2, Fig. 1). The

Table 1

Parasitoid species of *Liriomyza huidobrensis* on various plants and habitats (N: natural, U: urban, C: cultivated)

Parasitoid species	*Cucurbita maxima*			*Vicia faba*			*Arctium minus*			Rate (%) of parasitism
	N	U	C	N	U	C	N	U	C	
Eulophidae										
Chrysocharis caribea Bouček L/P[a]		X	X				X			<1
C. flacilla (Walker) L/P	X	X	X	X	X	X	X	X	X	34
C. vonones (Walker) L/P[a]	X		X	X	X	X	X	X	X	9
Chrysonotomyia Ashmead sp. L/L			X			X				<1
Diglyphus begini (Ashmead) L/L					X					<1
D. pedicellus Gordh & Hendrickson L/L						X				<1
D. websteri (Crawford) L/L					X	X	X		X	<1
Proacrias thysanoides (De Santis) L/L[a]			X		X	X	X	X	X	<1
P. xenodice (Walker) L/L[a]			X			X	X	X		<1
Pteromalidae										
Halticoptera helioponi De Santis L/P	X	X	X	X	X	X	X	X	X	27
Halticoptera Spinola sp. L/P							X			<1
Thinodytes Graham sp. L/P							X			<1
Eucoilidae										
Agrostocynips clavatus Diaz L/P	X	X			X	X	X	X	X	7
Braconidae										
Phaedrotoma luteoclypealis Van Achterberg & Salvo L/P[a]	X			X						<1
Ph. mesoclypealis Van Achterberg & Salvo L/P[a]	X									<1
Ph. scabriventris (Nixon) L/P		X	X	X	X	X	X	X	X	14

Host stage of oviposition/emergence indicated as L: larva, P: pupa.

[a] First record on *Cucurbita maxima*.

Table 2
Total, minimum, maximum and average (S.E.) number of species in the parasitic complex of *Liriomyza huidobrensis* in natural, urban and cultivated habitats (data obtained from experiments and sampling)

Host plant	Family	Natural			Urban			Cultivated		
		Total	Min–max	Mean (S.E.)	Total	Min–max	Mean (S.E.)	Total	Min–max	Mean (S.E.)
Cucurbita maxima	Braconidae	2	0–2	0.50 (0.50)	1	0-1	0.25 (0.25)	1	1	1
	Eucoilidae	1	0–1	0.25 (0.25)	1	0–1	0.25 (0.25)	0	0	0
	Eulophidae	2	1–2	1.50 (0.29)	2	0–2	1.25 (0.48)	6	0–6	1.60 (1.17)
	Pteromalidae	1	0–1	0.50 (0.29)	1	0–1	0.50 (0.29)	1	0–1	0.40 (0.24)
Vicia faba	Braconidae	2	0–1	0.75 (0.25)	1	0–2	0.50 (0.50)	1	1	1
	Eucoilidae	0	0	0	1	0–1	0.25 (0.25)	1	0–1	0.50 (0.29)
	Eulophidae	2	1–2	1.75 (0.25)	5	1–4	2.50 (0.65)	7	0–7	2.25 (1.65)
	Pteromalidae	1	0–1	0.75 (0.25)	1	0–1	0.25 (0.25)	1	0–1	0.75 (0.25)
Arctium minus	Braconidae	1	0–1	0.14 (0.10)	1	0–1	0.33 (0.21)	1	0–1	0.67 (0.21)
	Eucoilidae	1	0–1	0.64 (0.13)	1	0–1	0.33 (0.21)	1	0–1	0.17 (0.17)
	Eulophidae	6	0–6	1.43 (0.49)	4	1–3	2.00 (0.37)	4	0–4	1.50 (0.56)
	Pteromalidae	3	0–2	0.71 (0.19)	1	0–1	0.50 (0.22)	1	0–1	0.33 (0.21)

abundance of the most important parasitoid species varied significantly among environments for both plant species (*C. maxima* $\chi^2 = 121.87$, d.f. = 8, $P < 0.0001$; *V. faba* $\chi^2 = 525.47$, d.f. = 8, $P < 0.0001$). In cultivated habitats, more *P. scabriventris* and less *C. flacilla* than expected under independence of the variables were observed. Minor differences were observed among plant species (Table 3).

The analysis of variance did not detect important effects of year of sampling on any variable. Number of adults per leaf was similar across habitats for both plant species (0.4–1.5 adults per leaf in pumpkin $F_{4,7} = 2.41$, $P = 0.14$; and 0.5–0.8 adults per leaf in broad bean $F_{4,6} = 0.72$, $P = 0.51$). The average species richness in the complex associated with *L. huidobrensis* was similar in the three habitats and for both plant species. No significant difference in richness of particular families was detected (Table 2).

Average parasitism rates increased in the sequence natural < urban < cultivated, although differences were not significant (Fig. 2). In both plant species, parasitism by *P. scabriventris* was low in natural and urban habitats and significantly higher in crops (*C. maxima* $F_{4,7} = 8.48$, $P = 0.008$, *V. faba* $F_{4,6} = 10.74$,

Table 3
Total number of individuals obtained per host plant and habitat, expected figures from independence among variables in brackets

Host plant	Habitat	Parasitoid species					Total individuals
		Agrostocynips clavatus	*Chrysocharis flacilla*	*Chrysocharis vonones*	*Halticoptera helioponi*	*Phaedrotoma scabriventris*	
Cucurbita maxima	Natural	9[a] (4)	36[***] (17)	4 (2)	5 (3)	0[***] (28)	67
	Urban	6 (5)	26 (20)	0 (2)	4 (4)	27 (33)	65
	Cultivated	0[*] (6)	2[***] (27)	3 (3)	3 (5)	80[***] (46)	93
Vicia faba	Natural	0[*] (6)	86[*] (110)	60[***] (31)	50 (43)	17 (22)	218
	Urban	1[***] (17)	424[***] (314)	59[**] (89)	116 (123)	7[***] (64)	657
	Cultivated	27[***] (5)	9[***] (95)	28 (27)	38 (37)	81[***] (19)	215
Arctium minus	Natural	90[**] (65)	73 (92)	7 (13)	261[*] (226)	9[***] (45)	481
	Urban	3[*] (14)	12 (20)	8[**] (3)	57 (48)	14 (10)	109
	Cultivated	1[***] (15)	48[***] (22)	4 (3)	9[***] (53)	42[***] (11)	127

[a] Values deviating significantly from expected according to adjusted residuals (Chi-square test $P < 0.0001$) are marked with asterisks.

[*] $P = 0.05–0.01 > 1.95$ (adjusted residuals).

[**] $P = 0.01–0.001 > 2.575$ (adjusted residuals).

[***] $P < 0.001$ 5–10 > 3.3 (adjusted residuals).

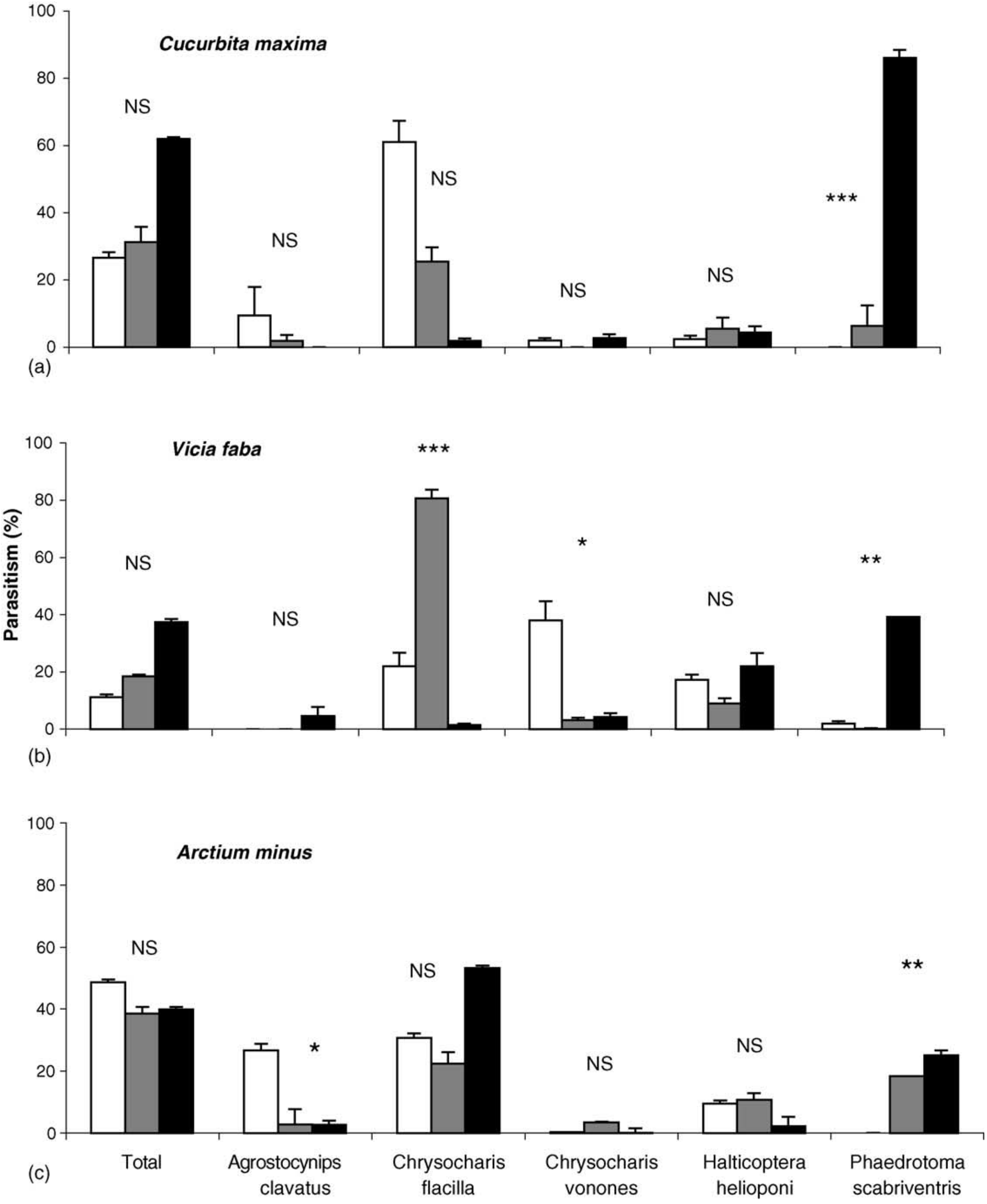

Fig. 2. Mean (±S.E.) total parasitism of *Liriomyza huidobrensis* in different habitats: natural (□), urban (▨) and cultivated (■) on *Cucurbita maxima* (a), *Vicia faba* (b) and *Arctium minus* (c). Probabilities above bars are according to nested ANOVA (NS = no significant difference; $^{*}P = 0.05$–0.01, $^{**}P = 0.01$–0.001, $^{***}P < 0.001$).

Table 4
Results of covariance analysis, performed with species richness (log) of parasitoid categories as dependent variables, habitat type as main factor, and sample size (log) as covariate

Species richness	Interaction[a]/main factor[b]/covariate[c]	F	d.f.	P
Total	Habitat × sample size	0.523	2,20	0.60
	Habitat	1.378	2,22	0.27
	Sample size	75.22	1,22	<0.001
Braconidae	Habitat × sample size	0.073	2,20	0.92
	Habitat	10.901	2,22	<0.001
	Sample size	16.493	1,22	<0.001
Eucoilidae	Habitat × sample size	0.958	2,20	0.60
	Habitat	2.984	2,22	0.07
	Sample size	6.120	1,22	0.02
Eulophidae	Habitat × sample size	0.732	2,20	0.49
	Habitat	1.075	2,22	0.36
	Sample size	23.076	1,22	<0.001
Pteromalidae	Habitat × sample size	0.972	2,20	0.40
	Habitat	1.417	2,22	0.26
	Sample size	21.847	1,22	<0.001

[a] All interactions proceed from preliminary models (main factor + covariate + interaction) for testing homogeneity of slopes.

[b] Statistics for main factor (habitat type) from the final model, with the interaction term removed.

[c] Statistics for covariate (sample size) from the final model, with the interaction term removed.

$P = 0.007$). The opposite was observed for parasitism by eulophids (Fig. 2).

Parasitism rates were not related to the number of parasitic species present. Discriminant analyses showed a significant divergence among parasitic assemblages of *L. huidobrensis* according to habitat type (Function 1: Wilks $\lambda = 0.066$, d.f. = 24, $P = 0.01$; Function 2: Wilks $\lambda = 0.405$, $\chi^2 = 13.99$, d.f. = 11, $P = 0.23$) (Fig. 3). No effect of plant species ($P = 0.21$) or year of replication ($P = 0.23$) was detected.

Leaves collected from the naturally mined weeds provided a total of 1680 adults, with 43% parasitoids belonging to 12 species and five families (Table 1). Parasitic complex from natural locations had a higher number of parasitic species but cultivated habitats had higher parasitism rates (Table 1). The composition of the parasitic complex associated with *A. minus* varied among habitats, the association between parasitoid species abundance and habitat type being highly significant ($\chi^2 = 250.93$, d.f. = 8, $P < 0.0001$) (Table 3).

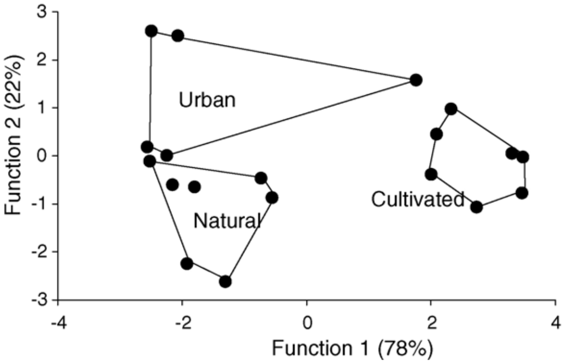

Fig. 3. Discrimination of parasitic assemblages based on habitat, using the abundance of parasitoid species in the parasitic complexes of *Liriomyza huidobrensis* from experiments and analysed with discriminant analysis.

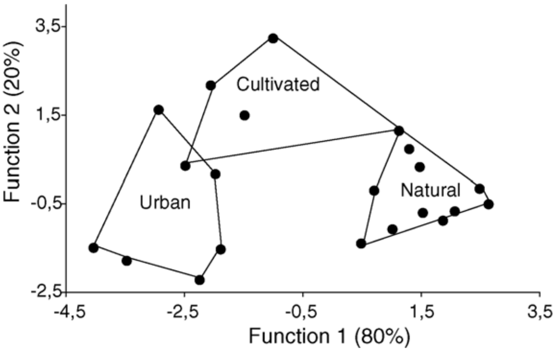

Fig. 4. Discriminant analysis based on the relative abundance of parasitoid species from 25 parasitic complexes obtained from *Liriomyza huidobrensis* on the weed *Arctium minus* in different habitats.

ANCOVA showed that total parasitoid richness was not affected by habitat type ($F_{2,22} = 1.37$, $P > 0.05$). Braconidae species richness was significantly higher in crops and urban localities than in natural ones, even after removing the effect of sample size (Table 4).

Total average parasitism, and parasitism caused by *C. flacilla*, *C. vonones*, and *H. helioponi* were similar among habitats. Parasitism by *P. scabriventris* was higher in cultivated and urban habitats than in natural ones (Fig. 2), by *A. clavatus* higher in natural localities. Discriminant analysis indicated a significative separation among parasitic complexes obtained in natural habitats versus managed environments (Function 1: Wilks $\lambda = 0.106$, d.f. = 20, $P = 0.006$; Function 2: Wilks $\lambda = 0.510$, d.f. = 9, $P = 0.23$) (Fig. 4).

4. Discussion and conclusions

In the parasitoid–herbivore system studied, the expectation that natural habitats offer better conditions than cultivated ones may be limited by other factors. Despite disturbances, the resource concentration in cultivated habitats had a beneficial effect on richness and abundance of *L. huidobrensis* parasitoids. The parasitism of *L. huidobrensis* increased in the sequence natural < urban < cultivated for both experimentally exposed plants and naturally occurring weeds. Small populations of leafminer larvae experimentally located in cultivated habitats attracted the highest total number of parasitoid species.

The leafminer develops high densities in both urban areas and horticultural crops, where the majority (91%) of its ornamental and cultivated host plants are found (Valladares and Salvo, 1999). In native habitats *L. huidobrensis* attacks six plant species only: *Datura ferox* L., *Hydrocotyle* sp., *A. minus*, *Bidens* sp., *Crepis pulchra* L. and *Sonchus oleraceus* L. (Salvo, 1996; Valladares, unpublished data). This overall picture was expected for a pest in its native habitat; where outbreaks only occur in cultivated or disturbed habitats, or on a susceptible exotic host plant (Mc Clure, 1997). Differences in host abundance have been mentioned as the main factor affecting patterns of parasitoid species richness, particularly for generalist parasitoids (Sheehan, 1994) and this could be the main reason for the increased parasitoid activity in cultivated habitats.

Leafminer parasitoids are dominated by generalist species (Salvo and Valladares, 1999) that tend to aggregate where a particular host is abundant, creating a ‘‘switching behaviour’’ between elements of their diet (Murdoch, 1969). In some parasitoid species, associative learning allows the individuals to focus on the most reliable cues in the environment (Hassell, 2000; Meiners et al., 2003). In cultivated habitats, parasitoids of leafminers could be adapted to search and exploit the most abundant host (Valladares and Salvo, 1999), whereas in natural habitats they may search for other, more abundant host species.

The high parasitism in cultivated habitats may be due to the diversity of plant species in the horticultural sites of the study area, which generally have wide natural margins and little chemical weed control (Valladares et al., 1999). Polycultural systems appear to be favourable habitats for increasing natural enemies (Risch et al., 1983; Andow, 1991) and weeds are known as reservoirs for leafminer parasitoids (Murphy and La Salle, 1999).

Most of the parasitoid species recorded on *L. huidobrensis* occurred in all habitat types, but their numerical proportion in the parasitic complexes varied significantly among habitats. Strong departures from a random distribution of particular parasitoid species were observed according to habitat type, some of them being common to both plant species used. The braconid *P. scabriventris* was notably more abundant in cropped areas, not only in field experiments, but also on *A. minus*.

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