



Temporal variation in the response of parasitoids to agricultural landscape structure

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Received 13 February 2002; received in revised form 3 January 2003; accepted 12 January 2003

Abstract

Temporal variations in the relationship between agricultural landscape complexity and parasitoid abundance were assessed in Ingham County, MI. The study site consisted of a 3.2 km × 13.9 km area including a complex and a simplified agricultural landscape. Landscape structure was quantified using black and white aerial photographs and digital land-use data. A heterogeneous mixture of crop and non-crop habitats characterized the complex landscape (40.6% of non-crop habitat), while the simple landscape was more uniform and contained less non-crop habitat (28.6%). In the complex landscape fields were 75% smaller, had 63% more perimeter of wooded field edge per hectare of field area, and 81% more field edge in wide hedgerow than in the simple landscape.

In June–July 1993, 1996, 1998, 2000, and 2001, a total of 15,786 armyworm (*Pseudaletia unipuncta*) larvae were released into maize fields. A total of 3752 larvae were recovered and reared in the laboratory with 1410 individuals parasitized by 15 identified species of parasitoids. Two species, *Glyptapanteles militaris* and *Meteorus communis*, represented 96.3% of the parasitoids recovered. Agricultural landscape structure influenced the temporal dynamics of *P. unipuncta* parasitism. While *G. militaris* was equally present in the simple (48.8% of total recovery) and complex landscape (51.2%), *M. communis* was found mostly in the complex landscape (78.9%). Overall, percentage parasitism differed between landscapes and among years with different trends in the simple and complex landscapes. These results indicate that effects of landscape structure on parasitism are not adequately characterized by short-term studies.

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Keywords: Agro-ecosystems; Landscape complexity; Temporal patterns; Parasitism; *Pseudaletia unipuncta*

1. Introduction

There is increasing evidence that habitat fragmentation can disrupt host–parasitoid relationships (Roland, 1993; Kruess and Tscharntke, 1994, 2000;

Roland and Taylor, 1997; Cappuccino et al., 1998; Thies and Tscharntke, 1999; Tscharntke, 2000). This is particularly important in annual cropping systems where the current tendency of removing hedgerows, fencerows, and woodlots generates highly simplified agricultural landscapes composed by intensively disturbed early successional systems (Auclair, 1976; Pogue and Schnell, 2001).

In cropping and non-cropping systems, several authors have reported year-to-year oscillations in

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parasitoid species richness and percentage parasitism (Askew and Shaw, 1989; West and Miller, 1989; Onstad et al., 1991; Hawkins, 1994; Cossentine and Jensen, 1995; Jones and Weinzierl, 1997). Incorporating a temporal perspective in the study of the impact of landscape structure on parasitoid dynamics is therefore a necessary step to conserve beneficial organisms in highly fragmented agroecosystems. However, the vast majority of previous research on the relationship between landscape structure and parasitoid abundance has been conducted during a relatively short amount of time (Marino and Landis, 1996; Golden and Crist, 1999; Menalled et al., 1999; Costamagna, 2002) or has not explicitly included 'time' as a variable of analysis (Roland and Taylor, 1997).

An assessment of the effect of landscape structure on parasitism of the armyworm, *Pseudaletia unipuncta* Haworth (Lepidoptera: Noctuidae), a common pest of small grains and grasses, allowed to postulate that when the proper habitat structural diversity is provided, parasitism increases with landscape complexity (Marino and Landis, 1996). Another study suggested that the factors responsible for the differences in parasitism between complex and simple landscapes (Marino and Landis, 1996) could be operating on relatively long time scales (Menalled et al., 1999).

This paper presents results of a large-scale, multi-year study aimed at understanding the impact of agricultural landscape structural diversity on rates of parasitism and parasitoid species abundance. It specifically examines: (1) if agricultural landscape structure affects parasitoid species richness, (2) if rate of parasitism changes over time, (3) if such a change is related to landscape complexity, and (4) if the impact of habitat structure varies between parasitoid species.

2. Methods

This study was conducted in a 3.2 km × 13.9 km area located in Leslie and Onondaga Township, Ingham County, MI, USA (42°25'30"N, 84°29'00"W). This area comprised two typical agricultural landscapes of southern Michigan, where the southernmost sector consisted of a complex landscape and the northernmost of a more simplified one. Landscape characterization was performed using black and white aerial photographs (1:2000) taken on June

1988 by the Michigan Department of Natural Resources (Lansing, MI, USA). Photos were scanned at 59 dots/cm and analyzed with ERDAS (Earth Resource Data Analysis System) 7.5 (ERDAS, Atlanta, GA, USA). Within each landscape, a land use classification at a multi-field scale was done using digital land-use data from the Michigan Department of Natural Resources, Michigan Resource Inventory System (MIRIS). Each studied landscape comprised an area of 3.2 km × 3.2 km and landscapes were separated by a 7.5 km × 3.2 km transitional area (cf. Marino and Landis, 1996; Menalled et al., 2000). During this study no major change in structural complexity was observed in either landscape. This study was conducted in only one simple and one complex agricultural landscape, and results should therefore be extrapolated cautiously.

In each of 1993, 1996, 1998, 2000, and 2001 three representative first year maize (*Zea mays* L.) fields under a corn–soybean rotation were selected in the complex and the simple landscape (for a total of 30 fields). For each field, three edges were selected at random and 100 m transects were established along the boundary between the selected field edge and the surrounding vegetation. Height of the field border vegetation was measured using a clinometer at 20 m interval (five regularly spaced points). At the same five 20 m intervals, width of the field border vegetation was measured up to 20 m and plant species composition was characterized with the point intercept method using 20 m transects running perpendicular from each field edge into the bordering vegetation (Bonham, 1989). Differences in vegetation height, border width, and species richness between the simple and the complex landscape were evaluated using a two-factor (landscape and year) ANOVA model.

Rates of parasitism of *P. unipuncta* were estimated in 1993, 1996, 1998, 2000, and 2001 in the same 30 fields used to characterize the extra-field vegetation. Marino and Landis (1996) and Menalled et al. (1999) provide a description of the biology of *P. unipuncta* and its parasitoids. Within each field, second to fourth instars of *P. unipuncta* obtained from a laboratory colony were released three times in June–July. Release sites consisted of three rows of 20 healthy maize plants and were 25 m apart. In 1993, *P. unipuncta* larvae were released in the field 5 and 90 m from field edges. Since no difference in percentage parasitism was detected,

Table 1
Dates and numbers of larval *P. unipuncta* released and recovered, and number of parasitoids obtained in Michigan, USA

Year	Landscape type	First release/last recovery date	Number of <i>P. unipuncta</i> released	Number of <i>P. unipuncta</i> recovered	Number of parasitoids reared
1993	Simple	17 June/5 July	3000	432	27
	Complex	17 June/5 July	3000	655	137
1996	Simple	25 June/16 July	999	287	17
	Complex	25 June/16 July	999	138	45
1998	Simple	19 June/9 July	1125	494	161
	Complex	19 June/9 July	1115	507	123
2000	Simple	15 June/13 July	1682	265	200
	Complex	15 June/13 July	1706	426	249
2001	Complex	13 June/3 July	1080	245	186
	Simple	13 June/3 July	1080	303	265

all following releases were conducted at 27 m (based on the smallest field used in the study in 1996). One insect per maize plant was liberated each time using a new set of plants for each release. First and last dates of release, number of *P. unipuncta* larvae released and recovered, as well as the number of parasitoids reared per landscape type and year are presented in Table 1.

Larval *P. unipuncta* were left in the field for 5–7 days and recovered by carefully inspecting maize plants in the release sites. Recovered larvae were individually placed in 30 ml plastic cups containing approximately 10 ml of artificial diet and were reared in the laboratory at 26 °C, 60% RH, under a 16:8 h (L:D) photoperiod. Each larva was inspected every 2–6 days to record stage of development, disease status, and parasitoid emergence. Parasitoids that emerged were identified by larval and cocoon remains (Guppy and Miller, 1970) and adult characteristics. Because the time larvae were left in the field differed among years, daily percentage parasitism was calculated (number of larvae parasitized \times 100/number of larvae released \times number of days they were left in the field).

For each year, overall daily percentage parasitism and daily percentage parasitism by species were analyzed using a two-factor (landscape and year) ANOVA model. Field effect was modeled as a random effect nested in landscape and year. To meet the assumptions of the ANOVA model, percentage parasitism data were arc-sin transformed before analysis (Sokal and Rohlf, 1995). Because of the existence of significant interactions between year

and landscape effects, post-ANOVA multiple comparisons were done through the slicing of the main effects.

3. Results

Fields in the complex landscape were on average 75% smaller, had 63% more perimeter of wooded field edge per ha of field area, and had 81% more field edge in wide hedgerow than those in the simple landscapes. Fields in the simple landscape had 74 and 53% more field edge in herbaceous roadside and crop-to-crop interface, respectively, than those in the complex landscape (cf. Marino and Landis, 1996).

Fields in the complex landscape were surrounded by taller vegetation (mean 9.97 ± 0.48 m) than those in the simple landscape (mean 2.61 ± 0.33 m) (landscape effect: $P < 0.0001$, year effect: $P < 0.1338$, landscape \times year: $P < 0.04$). Field borders were wider in the complex landscape (mean 15.3 ± 0.48 m) than in the simple landscape (mean 5.75 ± 0.44 m) (landscape effect: $P < 0.0001$, year effect: $P < 0.1866$, landscape \times year: $P < 0.6597$). The complex landscape contained more tree species (particularly *Prunus serotina* Ehrh.) than the simple landscape.

Of the 15,786 *P. unipuncta* larvae released into maize fields, 3752 larvae were recovered and 1410 individuals (37.6%) were parasitized (Table 1). A total of 15 species of parasitoids were identified (Table 2). Two braconid species *Glyptapanteles militaris* (Walsh) and

Table 2

Abundance of parasitoids recovered from *P. unipuncta* larvae released 1993–2001 in a simple and a complex agricultural landscape located in Leslie and Onondaga Townships, Ingham Co., MI, USA

Family	Species	Simple landscape						Complex landscape					
		1993	1996	1998	2000	2001	Total	1993	1996	1998	2000	2001	Total
Braconidae	<i>M. communis</i>	12	7	5	2	45 ^a	71	128	39	58	2	38 ^a	265
Braconidae	<i>G. militaris</i>	13	3	140	196	146	498	5	4	45	244	224	522
Braconidae	<i>Diclogaster auripes</i>	–	–	–	–	–	–	2	–	–	–	–	2
Ichneumonidae	<i>Therion sassacus</i>	1	–	–	–	–	1	–	1	–	–	–	1
Ichneumonidae	<i>Nepiera marginata</i>	1	–	–	–	–	1	–	–	–	–	–	–
Ichneumonidae	<i>Campoletis oxylus</i>	–	–	–	–	2	2	–	–	–	–	2	2
Ichneumonidae	<i>Campoletis</i> sp.	–	2	–	1	–	3	–	–	–	1	–	1
Ichneumonidae	<i>Ichneumon</i> sp.	–	5	–	–	–	5	–	–	–	–	–	–
Ichneumonidae	<i>Enicospilus purgatus</i>	–	–	8	–	–	8	–	–	6	–	–	6
Ichneumonidae	<i>Netelia sayi</i>	–	–	–	–	–	–	–	–	2	–	–	2
Eulophidae	<i>Euplectrus mellipes</i>	–	–	–	–	–	–	–	1	–	–	–	1
Tachinidae	<i>Winthemia rufopicta</i>	–	–	6	–	–	6	–	–	10	–	–	10
Tachinidae	<i>Periscepsia helymus</i>	–	–	–	–	–	–	1	–	–	–	–	1

^a In 2001, a subsample ($n = 95$) revealed that *M. dimidiatus* (Cresson) represented 5.3%, and *M. hyphantriae* Riley 3.2% of the specimens recorded as *M. communis*. In previous years only *M. communis* has been identified. An additional two unidentified tachinid species (eight individuals) were recovered.

Meteorus communis (Cresson), represented 72.4 and 23.9%, respectively, of the parasitoids recovered. Parasitism by *G. militaris* was similar in the simple and complex landscape (48.8 and 51.2% of total recovery,

respectively), whereas 78.9% of *M. communis* recovered were found in the complex landscape.

Among years, daily overall parasitism rates varied from 1.1 to 12.3% in the simple landscape and from

Table 3

Influence of agricultural landscape structure on overall percentage parasitism of *P. unipuncta* larvae, and on the two main parasitoid species in Ingham County, MI, over five sampling seasons (1993–2001)

	d.f.	Overall parasitism		<i>G. militaris</i>		<i>Meteorus</i> spp.	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
(a) Source of variation ^a							
Landscape structure	1	14.02	<0.01	3.05	0.10	30.23	<0.01
Year of sampling	4	119.17	<0.01	141.30	<0.01	56.92	<0.01
Landscape structure × year of sampling	4	12.01	<0.01	6.09	<0.01	14.13	<0.01
(b) Effect of year ^{b,d}							
Complex	4	47.68	<0.01	80.31	<0.01	58.90	<0.01
Simple	4	83.50	<0.01	67.09	<0.01	12.15	<0.01
(c) Landscape structure effect ^{c,d}							
1993	1	12.47	<0.01	0.38	0.57	17.59	0.01
1996	1	30.23	<0.01	0.59	0.45	32.57	<0.01
1998	1	2.22	0.16	17.19	<0.01	5.84	0.03
2000	1	5.63	0.04	3.11	0.10	0.41	0.53
2001	1	5.45	0.07	4.71	0.06	0.13	0.73

^a ANOVA: field (landscape × year) effect tested with residual error; landscape, year, and landscape × year effects tested with field (landscape × year) mean square.

^b Landscape × year effect sliced by landscape.

^c Landscape × year effect sliced by year.

^d Field (landscape × year) used as error.

4.0 to 14.7% in the complex landscape. Overall, percentage parasitism differed between landscapes and among years (Table 3a). The temporal dynamics of percent parasitism showed different trends in the simple and the complex landscape, with a significant year × landscape interaction (Table 3a). When data were sliced by landscape, results showed that mean percent parasitism varied significantly from year to year in both the complex and simple landscape (Table 3b). Analysis of the landscape × year effect sliced by year showed that percent parasitism was significantly higher in the complex landscape than in the simple landscape in 1993 and 1996, and marginally significant in 2001 ($P = 0.07$) (Table 3b). The same

analysis showed no significant difference between the simple and the complex landscapes in 1998, but significantly more parasitism in the simple landscape in 2000 ($P = 0.04$) (Table 3b). When data were sliced by landscape, results showed that mean percent parasitism varied significantly from year to year in both the complex and simple landscape (Table 3c).

Percent parasitism by *G. militaris* and *M. communis* differed between landscapes and years (significant year × landscape interaction, cf. Table 3a). The slicing of the data by landscape indicated significant year-to-year variations in the abundance of *M. communis* and *G. militaris* in both landscape types (Table 3b, Fig. 1a and b). Evaluation of the landscape × year

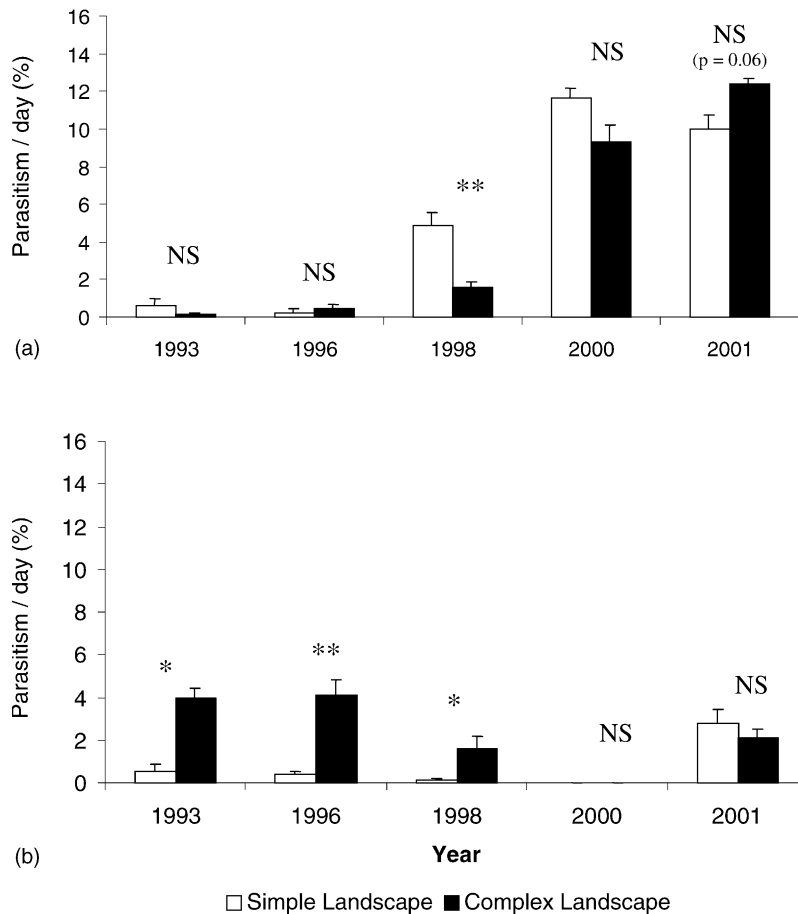


Fig. 1. Daily percentage parasitism (mean ± S.E.) of *P. unipuncta* by (a) *G. militaris*, and (b) *M. communis*, in a simple and a complex agricultural landscape in southern Michigan. Landscape × year effect sliced by year are indicated as ** $P < 0.01$, * $P < 0.05$, NS $P > 0.05$. In Fig. 1(b), we did not show bars for 2000. That is because we only collect 3 individuals, but the bars should still show up as in this graph: values for 2000 were 0.76 ± 0.38 , and 0.42 ± 0.23 (means % parasitism/day ± SE) for the simple and complex landscape, respectively.

effect sliced by year showed that percent parasitism by *G. militaris* was not significantly different between the complex and the simple landscape in 1993, 1996, and 2000 (Table 3c, Fig. 1a). In 1998, significantly more *G. militaris* were found in the simple than in the complex landscape, but in 2001 the opposite outcome was found, although the effect was only marginally significant (Table 3c, Fig. 1a). A different pattern was detected for *M. communis* with significantly more individuals collected in the complex than in the simple landscape in 1993, 1996, and 1998 (Table 3c, Fig. 1b). In 2000 and 2001, no significant differences were found in the recovery of *M. communis* between landscape types (Table 3c, Fig. 1b).

4. Discussion and conclusions

Many parasitoid species require resources such as plant nectar, pollen and secretions from scales and aphids. Since these resources are typically found in late successional habitats, Marino and Landis (1996) hypothesized that the abundance of woodlots, hedgerows, and fencerows within agricultural landscapes would be positively correlated with parasitoid species richness. The results presented here (1410 parasitoids with 11 species identified in the simple landscape, 13 species in the complex landscape) do not clearly support this hypothesis. An association between parasitoid species richness and agricultural landscape complexity could perhaps be detected in landscapes that contain more extreme differences.

Overall percentage parasitism was larger or at least equal in the complex compared to the simple landscape in 4 of the 5 years of the study, while it was higher in the simple landscape during 2000. *Glyptapanteles militaris* showed a peak of abundance in the last 2 years of the study in the simple landscape, whereas *M. communis* was the dominant species in the complex landscape during the first 3 years of this study. *Glyptapanteles militaris* primarily parasitizes Noctuidae in maize and herbaceous non-crop habitats (Calkins and Sutter, 1976; Covell, 1984), a type of environment present in both the complex and simple agricultural landscapes. On the other hand, *P. serotina* is a host plant to five of the seven reported hosts of *M. communis* (Krombein et al., 1979; Covell, 1984). The low abundance of *P. serotina* in the simple landscape may explain the low

populations of *M. communis* in that area. Conversely, the relatively high abundance of *P. serotina* in complex agricultural landscapes may account for the increased presence of *M. communis* in this area (Marino and Landis, 1996; Menalled et al., 1999). The relatively high numbers of *M. communis* collected in both landscapes during the last year of the study were coincident with an outbreak of *P. unipuncta* in Michigan (DiFonzo, 2001). It is possible that unusually high numbers of *P. unipuncta* might allow *M. communis* to extend its distribution to areas in the simple landscape with otherwise few hosts.

To fully understand the relationship between habitat structural complexity and host–parasitoid dynamics it is necessary to assess how this relationship varies over time. It is unclear why *G. militaris* showed a peak of abundance in 1998, 2000 and 2001, while *M. communis* abundance remained constant throughout the first half of this study to decline in 1998 and 2000, and reappear in both systems in 2001. Additional information is therefore needed on the potential effects of host density on parasitism and on existence of interspecific competition for hosts (Hawkins, 2000).

Acknowledgements

We thank the Landis Lab personnel for assistance in the field studies. W. Showers, D. Gunnerson, L. Lewis and J. Dyer of Iowa State University supplied *P. unipuncta* larvae. P. Dixon, Iowa State University, provided statistical advice. A. Ziegler and S. Gage, Michigan State University, Entomology Spatial Analysis Laboratory, assisted us in the landscape characterizations. We thank M. Sharkey for identification of the Braconidae, M. Wood and J. O'Hara for identification of the Tachinidae, and J. Luhman for identification of Ichneumonidae and Braconidae. We acknowledge G. Bailey, R. Cover, R. DeBruler, L. Eldred, S. Hawkins Jr., C. Priest, and D. Swiler, for the use of their fields. We thank M. Liebman, P. Barbosa, and two anonymous reviewers for their comments and suggestions. This research was funded by USDA SARE grants LWF 62-016-03508 and LNC 95-85, USDA LISA grant 62-016-02942, and a grant from the National Science Foundation's Long-Term Ecological Research (LTER) program on agricultural ecology at Michigan State University (DEB-92-11771).

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