

## DOES AGRICULTURAL LANDSCAPE STRUCTURE AFFECT PARASITISM AND PARASITOID DIVERSITY?

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**Abstract.** This study evaluates whether previous observations of a higher percentage of parasitism and parasitoid diversity in a complex agricultural landscape, relative to a simple landscape, represent a general phenomenon. Rates of parasitism and parasitoid diversity of the armyworm (*Pseudaletia unipuncta*) were assessed in three replicate (Onondaga, Ingham, and Benton) regions in southern Michigan. Within each region, a simple landscape (primarily cropland) and a complex landscape (cropland intermixed with mid and late successional noncrop habitats) were identified through analysis of aerial photographs. In each landscape, three maize fields were selected, and second to fourth instar *P. unipuncta* were released into three replicate plots of maize plants. Larvae were recovered after 6 d and reared in the laboratory to record parasitoid emergence. A principal component analysis conducted on landscape variables indicated that simple and complex landscapes were true replicates. Extra-field vegetation was similar among the three simple landscapes but differed among complex sites. Parasitoid species diversity differed among regions, with six species recovered in Onondaga and two species from both Benton and Ingham. Rates of parasitism were only partially consistent with previous experimental results. In Ingham, results were similar to those found previously in this region; rates of parasitism and parasitoid diversity were higher in the complex landscape. However, in Onondaga and Benton, no difference in rates of parasitism or parasitoid diversity were found. Thus, the hypothesis that landscape complexity increases parasitoid diversity and rates of parasitism was not supported. Possible reasons for the observed differences in rates of parasitism among regions are discussed.

**Key words:** agroecosystems; alternate hosts; extra-field vegetation; landscape structure; parasitism; parasitoid diversity; *Pseudaletia unipuncta*; spatial replication.

### INTRODUCTION

Insect parasitoids comprise a diverse set of taxa with the potential to regulate populations of many pest insects (Hassell 1986, LaSalle 1993). However, the simplified physical structure of many agricultural landscapes may be unfavorable to those parasitoid species that require resources found only in noncrop habitats (Townes 1972, Landis and Menalled 1998). In particular, the agricultural landscapes of the north temperate United States have been altered from an original matrix of primarily mid to late successional habitats interspersed with fragments of early successional habitats, to a matrix of primarily intensively disturbed early successional habitats interspersed with fragments of later successional habitats (Auclair 1976). Such landscape changes can influence the richness and effectiveness of natural enemy communities (Szentkiralyi and Kozar 1991), including parasitoid communities (Corbett and Rosenheim 1996, Marino and Landis 1996).

To maximize parasitoid survival in agroecosystems,

resources such as alternate hosts, food for adults (e.g., pollen and nectar), accessibility of overwintering habitats, constant food supply, and appropriate microclimates must be present (van Emden 1965a, b, 1990, Rabb et al. 1976, Powell 1986, Debach and Rosen 1991, Dyer and Landis 1996, 1997). These resources may occur within fields through intercropping (Dempster and Coaker 1974, Perrin 1977, Altieri et al. 1978), or by promoting the existence of a weedy background (Dempster 1969, Tahvanainen and Root 1972, Foster and Ruesink 1984). Resources for natural enemies may also occur at a larger, between-field scale, through the presence of hedgerows, woodlots, and oldfields (van Emden 1965a, b, Sotherton 1984, 1985, Coombes and Sotherton 1986).

To determine if the complexity of agricultural landscape structure influenced parasitoid species richness and overall percentage parasitism, Marino and Landis (1996) used the armyworm, *Pseudaletia unipuncta* Haworth, as a model host insect. Second–fifth instar *P. unipuncta* were released onto maize plants (*Zea mays* L.) growing in fields located either within a complex or within a simple agricultural landscape in central Michigan, USA. While parasitoid species diversity did

Manuscript received 17 February 1998; revised 24 July 1998; accepted 27 July 1998.

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not differ between landscape types, mean percentage parasitism was significantly higher in the complex landscape than in the simple landscape (13.1% vs. 2.4%). This difference was due almost exclusively to the presence of a generalist braconid, *Meteorus communis* Cresson. Because Marino and Landis (1996) did not replicate simple and complex landscapes, their conclusions regarding landscape influence on parasitism were limited to the area under study. In this study, we replicated landscapes by selecting three regions in central Michigan, each containing a simple and a complex landscape. We did this to assess whether Marino and Landis' (1996) observation of higher percentage parasitism in complex agricultural landscapes represents a more general phenomenon. Our expectation was that any difference between simple and complex landscapes in parasitism and/or parasitoid diversity would be consistent across regions.

#### MATERIALS AND METHODS

##### *Landscape analysis*

Three replicate regions comprising typical agricultural landscapes of central Michigan, USA were selected for this study: (1) Onondaga Township, Ingham County, Michigan (42°25' N, 84°29' W, hereafter Onondaga), (2) Ingham Township, Ingham County, Michigan (42°35' N, 84°20' W, hereafter Ingham), and (3) Benton Township, Eaton County, Michigan (42°40' N, 84°55' W, hereafter Benton). The Onondaga region was the same one studied by Marino and Landis (1996). Regions were 18–34 km apart from one another and were selected to contain a highly heterogeneous mixture of crop and noncrop habitats (hereafter "complex landscape") and a homogenous area with low crop diversity and few noncrop habitats (hereafter "simple landscape"). Within each region, the simple and the complex landscape were  $\geq 10$  km<sup>2</sup> and 6–9 km apart from one another.

Quantification of landscape structure was conducted by analysis of black and white aerial photographs (1:2000). Photos were taken on 12 June 1988 by the Michigan Department of Natural Resources (Lansing, Michigan, USA) for Onondaga and 14 April–12 May 1995 by the Tri-County Regional Planning Commission (Lansing, Michigan, USA) for Ingham and Benton. Photos from Onondaga were scanned at 150 dots per inch (dpi) and analyzed with ERDAS 7.5 (Earth Resource Data Analysis System, ERDAS, Atlanta, Georgia, USA). Photos of the Ingham and Benton regions were scanned at 300 dpi and analyzed using Image (ERDAS, Atlanta, Georgia, USA). By photo interpretation of the scanned images, all agricultural fields within each region–landscape combination were identified, and 30 fields from each combination were selected randomly for further analysis. The following attributes of each selected field were measured: area, perimeter, distance from field center to closest edge,

number of edge types (e.g., woods, hedgerow, fencerow, crop, and residential) per field, area to perimeter index, percentage of field perimeter comprising late successional habitats (woodlots, wide hedgerows [ $>10$  m wide], shrublands, and old fields) and percentage of field perimeter comprising early successional habitats (herbaceous roadside, crop, and residential). A principal component analysis (PCA) (ter Braak 1995; Proc Princomp, SAS Institute 1996) on standardized values of landscape variables was conducted to assess if there were differences in landscape characteristics across the three regions that could confound results. Percentage of field perimeter comprising early or late successional habitats was arcsine-transformed before the ordination.

##### *Extra-field vegetation*

In each region, three representative maize fields in the complex and three maize fields in the simple landscapes were chosen. For each field, three edges were selected randomly, and 100 m transects parallel to the field edges were established at the boundary between the selected field edges and the surrounding vegetation. Extra-field canopy height was measured at 0, 25, 50, 75, and 100 m along these transects using a clinometer. Canopy heights were analyzed using a three factor (region, landscape, and field) ANOVA model, with fields nested within landscapes (Proc GLM, SAS Institute 1996).

For each selected field edge, hedgerow species composition was characterized using a second set of five 15 m transects. These five transects were separated from one another by 25 m and run perpendicular from each field edge into the surrounding extra-field vegetation. Tree and shrub species composition was determined at 0, 5, 10, and 15 m along these transects using point transects (Bonham 1989). A PCA was used to ordinate vegetational composition and help visualize similarities and differences among landscapes and regions. To decrease the impact of rare species, the ordination was conducted using those species that had a relative abundance  $>2\%$ .

##### *Armyworm parasitism and parasitoid diversity*

*Pseudaletia unipuncta* was chosen as the target host, because it is an important crop pest throughout the North Central Region (NCR) of the United States and had previously been used successfully in a similar study by Marino and Landis (1996). *Pseudaletia unipuncta* has 35 potential parasitoids in the NCR, suggesting a potential for exploring parasitoid diversity differences between simple and complex landscapes. In this study, rates of parasitism of *P. unipuncta* were evaluated in the 18 fields (three fields per landscape and region) described. Within each field, armyworms were released at 27 m from those field edges chosen to characterize the extra-field vegetation. The distance of 27 meters from the field edge was chosen because this was the distance from the field edge to the center

TABLE 1. Date and number of armyworm larvae released per region and landscape.

Region	Landscape	1st release		2nd release		3rd release		Total released
		Date	Number released	Date	Number released	Date	Number released	
Onondaga	Simple	25 June	189	3 July	405	10 July	405	999
	Complex	25 June	189	3 July	405	10 July	405	999
Ingham	Simple	25 June	189	3 July	405	10 July	405	999
	Complex	25 June	189	3 July	405	10 July	405	999
Benton	Simple	26 June	189	9–10 July	540	24 July	675	1404
	Complex	26 June	189	9–10 July	540	24 July	675	1404

in the smallest field. At each field edge, three sites were established for the release of armyworms (three per field edge, for a total of nine sites per field). Release sites were separated from one another by 25 m and consisted of three rows of healthy maize plants. Armyworms obtained from a laboratory colony were released, one insect per maize plant, three times during the 1996 growing season, using a new site for each release. Release dates and number of armyworm larvae released per site are presented in Table 1. We used second–fourth instars (primarily second and third), because most larval parasitoids of *P. unipuncta* attack these stages (Guppy 1967).

Larvae were recovered 6 d after each release by carefully inspecting maize plants in the release sites. We observed no evidence of natural infestation by armyworms or other insects that could have influenced the abundance or searching of adult parasitoids. Thus, all armyworm larvae recovered were assumed to be those released for this study. Recovered larvae were placed individually into labeled 30 mL plastic cups containing approximately 10 mL of artificial diet. Larvae were returned to the laboratory and reared at 26°C, 60% relative humidity, and a photoperiod of 16:8 (light:dark) h. Larvae were observed every 4–6 d to record stage of development, disease status, and parasitoid or moth emergence. Parasitoids that emerged were identified by larval and cocoon remains (Guppy and Miller 1970) and adult characteristics. Data were combined across the three release dates and results were analyzed using a three factor (region, landscape, and field) ANOVA model, with fields nested within landscapes and percentage parasitism as the dependent variable. To meet assumptions of ANOVA, percentage parasitism was arcsine transformed before the analysis (Sokal and Rohlf 1995).

## RESULTS

### Landscape analysis

An ordination of the landscape variables indicated similar characteristics for complex and simple landscapes across regions (Fig. 1). Within each landscape type, it was not possible to differentiate fields belonging to the same region, suggesting that simple and complex landscapes across regions can be considered as true replicates. The first component (PC1) divided sim-

ple from complex landscapes with field area, field perimeter, and maximum distance from a field edge as the main variables responsible for the separation of groups (43% contribution to total variation). Fields in complex landscapes were smaller in area and had less perimeter and shorter maximum distance to field edge than those from simple landscapes (Table 2). The second component (PC2) accounted for 23% of the total variation, and gives a measure of the successional stage of surrounding vegetation, since it was positively related to perimeter comprised by late successional habitats and was negatively related to perimeter comprised by early successional habitats. Thus, fields in complex landscapes had a greater percentage of perimeter comprised by late successional habitats than fields in simple landscapes. Fields in simple landscapes were surrounded primarily by early successional habitats, such as crops or herbaceous plants. The mean number of edge types per field and the area to perimeter index was similar for simple and complex landscapes of the three regions (Table 2). No clear pattern could be detected for the third component (17% contribution to total variation).

### Extra-field vegetation

Results from ANOVA suggest that simple and complex landscapes differed in the height of the vegetation surrounding fields (mean  $\pm$  1 SEM; complex landscapes,  $9.6 \pm 0.5$  m; simple landscapes,  $2.1 \pm 0.3$  m) ( $df = 1$ ,  $F = 146.44$ ,  $P = 0.0001$ ). There were no significant differences between regions ( $df = 2$ ,  $F = 0.54$ ,  $P = 0.5838$ ), among fields nested within landscapes ( $df = 4$ ,  $F = 1.81$ ,  $P = 0.1268$ ), region  $\times$  landscape ( $df = 2$ ,  $F = 0.61$ ,  $P = 0.5434$ ), or a significant region  $\times$  field (landscape) interaction ( $df = 8$ ,  $F = 1.41$ ,  $P = 0.1946$ ). Ordination of species composition of field borders indicated different trends for simple and complex landscapes (Fig. 2) with complex landscapes containing more tree and shrub species per field ( $10 \pm 0.6$ , mean  $\pm$  1 SEM) than simple ones ( $2 \pm 1.5$ ). While species composition of field margins was similar among the three simple landscapes, complex areas were scattered along the first principal component (PC1, 22% contribution the total variation). While complex fields from Benton were located in the positive values of PC1, those from Onondaga were located

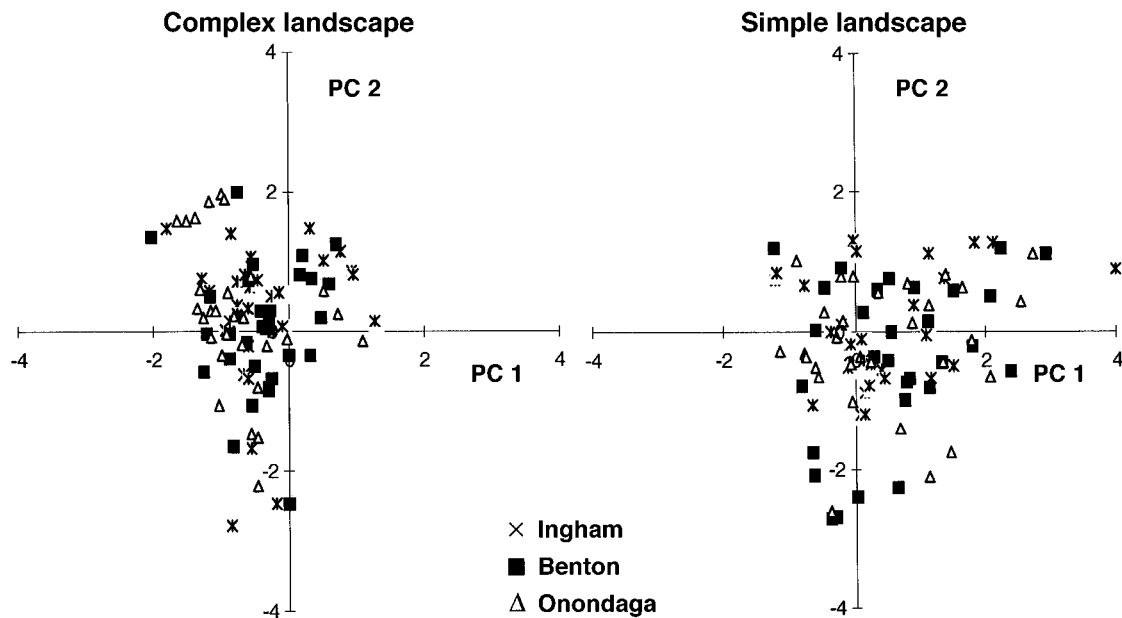


FIG. 1. Principal component (PC) analysis of structural variables of simple and complex landscapes from Onondaga, Ingham, and Benton. The first component (PC1) divided simple from complex landscapes with field area, field perimeter, and maximum distance from a field edge as the main variables responsible for the separation of groups. The second component (PC2) gives a measure of the successional stage of surrounding vegetation.

around its zero value, and those from Ingham were located at the negative values. *Ulmus* spp., *Fraxinus americana*, *Acer saccharum*, and *Quercus alba* were positively associated with PC1 and were found mostly in the fields of the complex landscape of Benton. The second principal component (PC2, 22% contribution to the total variation) separated fields from the complex landscapes of Ingham and Onondaga (positive values), from fields located in the complex landscape of Benton (zero and slightly negative values), and all fields located in simple landscapes (negative values). *Prunus serotina*, *Rubus occidentalis*, *Sassafras albidum*, and *Rhus copallina* were mainly associated with this PC2 and were found mostly in complex fields in Onondaga

and Ingham. Specifically, *Prunus serotina* was the most abundant species in complex fields of Onondaga. The third principal component (PC3) accounted for 12% of the total variability. *Ulmus americana* and *Tilia americana* had positive associations in this component and were found mostly in the complex landscape of Benton.

#### Armyworm parasitism and parasitoid diversity

A total of 1366 armyworm larvae were recovered. Six parasitoid species were recovered: four from fields located in simple landscapes and four from fields located in complex landscapes (Table 3). While six species were recovered from Onondaga, only two species were recovered from both Benton and Ingham. The

TABLE 2. Mean (1 SEM) of structural variables and percentage parasitism of simple and complex landscapes in central Michigan, USA. (Data for Onondaga modified from Marino and Landis [1996].)

Structural Variable	Ingham		Onondaga		Benton	
	Simple	Complex	Simple	Complex	Simple	Complex
Area (ha)	12.5 (1.7)	5.3 (0.7)	12.4 (1.9)	3.4 (0.6)	13.6 (1.9)	5.7 (0.8)
Perimeter (m)	1558 (110)	1044 (97)	1638 (131)	776 (55)	1651 (130)	1048 (85)
Area-to-perimeter I†	1.31 (0.02)	1.33 (0.04)	1.43 (0.05)	1.32 (0.04)	1.37 (0.03)	1.31 (0.04)
Maximum distance to edge (m)	120 (10)	77 (7)	101 (10)	63 (7)	111 (10)	74 (5)
No. of edge types per field	3.81 (0.21)	3.93 (0.25)	4.03 (0.21)	3.60 (0.24)	3.93 (0.20)	3.73 (0.19)
Percentage of perimeter in late successional habitats	33 (5)	48 (4)	29 (4)	47 (6)	28 (4)	46 (5)
Percentage of perimeter in early successional habitats	37 (4)	26 (5)	43 (5)	20 (4)	54 (6)	32 (4)
No. of larvae recovered	242	171	287	137	187	342
Percentage parasitism	3.3 (1.5)	3.8 (2.6)	3.7 (1.6)	29.8 (6.3)	2.4 (2.2)	0.9 (0.9)

†  $I = P/(2\sqrt{\pi A})$ . The value of  $I$  for different shapes are as follows: circle, 1.0; square, 1.1; rectangle (1 × 2), 1.2; rectangle (1 × 5), 1.3; rectangle (1 × 10), 1.9.

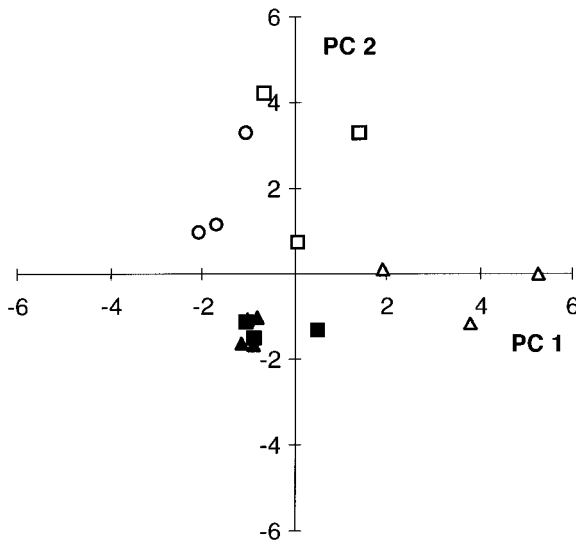


FIG. 2. Principal component analysis of vegetation surrounding fields in simple and complex landscapes.  $\Delta$  = fields from Benton complex landscape;  $\blacktriangle$  = fields from Benton simple landscape;  $\circ$  = fields from Ingham complex landscape;  $\bullet$  = fields from Ingham simple landscape;  $\square$  = fields from Onondaga complex landscape;  $\blacksquare$  = fields from Onondaga simple landscape.

native braconid *Meteorus communis* (Cresson) accounted for 72.5% of total parasitism (57.1% in the simple and 80.7% in the complex landscape). The highest percentage parasitism ( $29.8\% \pm 6.3$ , mean  $\pm$  SEM), and by far the highest number of parasitoids, were observed in the complex landscape of Onondaga. Very few parasitoids were reared from armyworm larvae recovered in either complex or simple landscapes within the Benton or Ingham regions. Percentage parasitism for each landscape–region combination is presented in Table 2. Due to the high differences in percentage parasitism among regions, we observed a significant region  $\times$  landscape interaction ( $df = 2$ ,  $F = 8.11$ ,  $P = 0.0012$ ) (Fig. 3). The analysis of the region  $\times$  landscape effect, sliced by region, indicated that the percentage parasitism was significantly higher in the complex landscape of Onondaga than in its simple landscape ( $df = 1$ ,  $F = 21.18$ ,  $P = 0.0001$ ), with no significant difference between the simple and the complex landscapes of both Benton and Ingham ( $df = 1$ ,  $F = 0.13$ ,  $P = 0.7194$  and  $df = 1$ ,  $F = 0.09$ ,  $P = 0.7698$ , respectively).

When data were sliced by landscape, mean percentage parasitism was significantly higher in the complex landscape of Onondaga than in the other two complex landscapes ( $df = 2$ ,  $F = 20.30$ ,  $P = 0.0001$ ) with no difference among the three simple landscapes ( $df = 2$ ,  $F = 0.41$ ,  $P = 0.6643$ ).

#### DISCUSSION

Ecological theory predicts higher insect diversity with increasing vegetational structure (Murdoch et al. 1972, Lawton and Schröder 1977, Southwood et al. 1979, Lawton 1983, Stinson and Brown 1983, Hawkins and Lawton 1987, Brown 1991), and parasitoid species richness has indeed been found to be positively correlated with plant architectural complexity (Askew 1980, Hawkins and Lawton 1987). Structurally diversity in landscapes may be especially critical for providing or increasing resources for natural enemies (Gut et al. 1982, Liss et al. 1986, Szentkiralyi and Kozar 1991, Landis and Haas 1992, Marino and Landis 1996). However, our results indicated that these observations cannot be regarded as generalizations that apply to all agroecosystems.

In this study, the percentage parasitism of *P. unipuncta* was significantly higher in the complex than in the simple landscape, only in Onondaga. Because Onondaga is the same region used by Marino and Landis (1996), we did confirm their observations of higher rates of parasitism of *P. unipuncta* in that particular complex landscape vs. the simple landscape. Indeed, observed rates of parasitism were twofold higher than values reported by Marino and Landis (1996). (Their findings were the following: complex, 13.1%; simple, 2.4%. In the current study we find the following: complex, 29.8%; simple, 3.7%.) The number and relative abundance of hymenopteran parasitoid species recovered from *P. unipuncta* were similar to values found by Marino and Landis (1996) and several previous studies (Breeland 1958, Pond 1960, Guppy 1967, Untung 1978, McNeil and Turgeon 1988). As discussed by Marino and Landis (1996), the choice of releasing early instars may have resulted in negligible rates of parasitism by most dipteran parasitoids, which attack the more difficult to recover fifth and sixth instars of *P. unipuncta*.

All six parasitoid species recovered from *P. uni-*

TABLE 3. Total number of parasitoids recovered from *Pseudaletia unipuncta* larvae released in simple and complex landscapes in central Michigan, USA.

Order: Family	Species	Onondaga		Benton		Ingham	
		Complex	Simple	Complex	Simple	Complex	Simple
Hymenoptera: Braconidae	<i>Meteorus communis</i> (Cresson)	39	7	1	1	2	8
Hymenoptera: Braconidae	<i>Glyptapanteles militaris</i> (Walsh)	4	3	...	2	4	...
Hymenoptera: Ichneumonidae	<i>Therion sassacus</i> Viereck	1	...	...	...	...	...
Hymenoptera: Ichneumonidae	<i>Camptopletis</i> spp.	...	2	...	...	...	...
Hymenoptera: Eulophidae	<i>Euplectrus mellipes</i> (Prov.)	1	...	...	...	...	...
Hymenoptera: Ichneumonidae	<i>Ichneumon</i> spp.	...	5	...	...	...	...



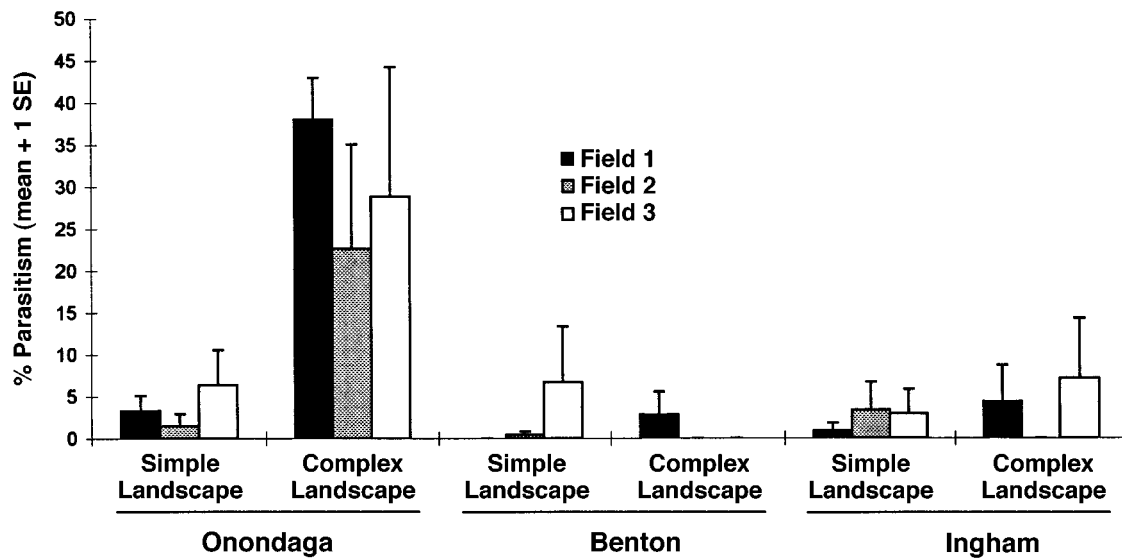


FIG. 3. Mean percentage parasitism of *Pseudaletia unipuncta* 27 m from hedgerow within maize fields in simple and complex landscapes, in three regions of southern Michigan, USA.

*puncta* are generalists. Askew and Shaw (1986) and Price (1991, 1994) proposed that generalist parasitoids are primarily adapted to search for hosts in late successional habitats. When studying the parasitoid communities of pest Lepidoptera in the North Central USA, Landis and Marino (*unpublished data*) showed that generalist parasitoids represent ~50% of the potential parasitoid community, with ~68% of the alternate hosts of generalist parasitoids also feeding in late successional habitats. Thus, by having a high proportion of a late successional habitats such as woodlots interconnected by hedgerows, complex agricultural landscapes may be expected to maintain higher abundance and diversity of generalist parasitoids than intensive agricultural areas with low crop diversity and few late successional noncrop habitats. In contrast to this prediction, the current study, as well as that of Marino and Landis (1996), observed mostly generalist parasitoids in both simple and complex agricultural landscapes. However, the selection of a generalist herbivore, *P. unipuncta*, in both cases may also explain the predominance of generalist parasitoids.

It is unclear why we found no difference in rates of parasitism between complex vs. simple landscapes in two of the three studied regions. Possible sources for the observed differences include the following: (1) landscape influences on parasitoid abundance and diversity occur at scales different than those measured, (2) extra-field vegetation imposes restrictions in parasitoid abundance and alternative hosts, and (3) population dynamics of parasitoids and/or alternative hosts may differ among regions.

Selection and characterization of simple and complex landscapes for this study were not based specifically on parasitoid requirements (i.e., microclimatic conditions, presence of food supply, and abundance of

alternate hosts); rather, they were selected to represent two contrasting environments resulting from farming activities. Although, at the level of resolution of our study and for the set of landscape variables we selected, landscapes can be regarded as true replicates of one another (Fig. 1), parasitoid abundance and diversity in agroecosystems may be affected by processes acting at different spatial scales. For example, Roland and Taylor (1997) observed that parasitoid species responded to forest fragmentation at different spatial scales and that this pattern was correlated with their relative body size. There are substantial logistical problems involved in assessing the extent to which agricultural landscape structure may alter host and parasitoid population dynamics, but future research should attempt to include a spatial approach that considers patterns and mechanisms of colonization and extinction.

The second explanation may be due to bottom-up influences of the vegetational structure of complex landscapes. Extra field-vegetation differed considerably among the three complex landscapes (Fig. 2), which may translate into variations in the abundance of alternative hosts of *M. communis*, the parasitoid species that accounts for 72.5% of total parasitism of *P. unipuncta* in this study. All alternative hosts of *M. communis*, except *Dargida procincta* Grote, which does not occur in Michigan, are exposed to larvae that feed primarily on trees and shrubs (Krombein et al. 1979, Covell 1984, Stehr 1987, West and Miller 1989, Marino and Landis 1996). It is known that *P. serotina* is a host plant for five of the seven hosts of the parasitoid *M. communis*, and it constituted the greatest proportion of tree species in the Onondaga region. Few *P. serotina* individuals were found in the other two complex landscapes. Future studies should explore the potential links between the presence of *P. serotina*, the abundance of

alternative hosts of *M. communis*, and how they influence rates of parasitism of *P. unipuncta*. Such a linkage between alternative hosts, specific plants in extra-field habitats, and increased rates of parasitism was observed by Corbett and Rosenheim (1996).

Finally, differences among regions in the temporal population dynamics of parasitoids and/or alternate host species may be responsible for the different rates of parasitism in the complex landscapes. West and Miller (1989) analyzed the patterns of host exploitation by *M. communis* in peppermint and alfalfa fields in Oregon, USA and found that average percentage parasitism was higher in 1985 than in 1984. Field observations from Michigan indicate that populations of alternative hosts of *M. communis* peak every 4–6 yr (M. Nielsen, *personal communication*). These observations coupled with our observation of changes in percentage parasitism in the complex landscape of Onondaga (13.1% in 1994 [Marino and Landis 1996] compared to 29.8% in the current study) are consistent with the hypothesis that periodic oscillation occurs in populations of alternative hosts.

Overall, the results of this study did not support the hypothesis that landscape complexity increases rates of parasitism and parasitoid diversity. The factors causing Marino and Landis (1996) to find differences in rates of parasitism between a complex and a simple landscape are complicated and not generalizable over the short term. We identified three possible causes for the observed departures from the predicted pattern of higher rates of parasitism in complex agricultural landscapes vs. simple ones. Examination of these causes will require studies across several spatial and temporal scales of the biology, realized host range, overwinter requirements, and microclimate requirements of generalist parasitoids and their alternate hosts (Shaw 1994, Corbett and Rosenheim 1996, Dyer and Landis 1996, 1997).

#### ACKNOWLEDGMENTS

We thank M. Haas, D. Carmona, J. J. Forester, and G. Hellmann for assistance in the field and L. Lewis and J. Dyer of Iowa State University for supplying armyworm larvae. A. Ziegler, Michigan State University, Entomology Spatial Analysis Laboratory assisted us in the landscape characterizations. We acknowledge S. Hawkins, Jr., J. Diehl, L. Eldred, D. Swiler, G. Pruden, D. Dankenbring, L. Woodworth, J. Caughey, and W. Garvey for the use of their fields. This research was funded by USDA SARE grant LWF 62-016-03508.

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