EFFECT OF LANDSCAPE STRUCTURE ON PARASITOID DIVERSITY AND PARASITISM IN AGROECOSYSTEMS[1]

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Abstract. The armyworm (*Pseudaletia unipuncta*) was used as a model host insect to explore the influence of agricultural landscape structure at two spatial scales on larval parasitoid species richness and rates of larval parasitism in southern Michigan. First, within fields, we compared parasitoid communities in maize fields near, and distant from, a hedgerow edge. Second, we replicated these studies within a complex landscape (agricultural fields of small size embedded in a landscape with abundant hedgerows and woodlots) vs. a simple landscape (agricultural fields of large size embedded in a landscape with few hedgerows and woodlots).

The structural differences between the simple and complex agricultural landscapes were characterized by analysis of aerial photographs and digital land-use data. After landscape analysis, three maize fields from each area were selected for the experimental studies. The complex landscape contained fields that were 75% smaller, had 63% more perimeter of wooded field edge per hectare of field area, and had 81% more field edge in wide hedgerow than fields in the simple landscape. Fields in the simple landscape had 74% and 53% more field edge in herbaceous roadside and crop-to-crop interfaces, respectively, than did fields in the complex landscape.

In the six selected maize fields, third and fifth instar *P. unipuncta* were released individually onto maize plants 5 m and 90 m from a hedgerow edge. Larvae were recovered after 4–5 d and reared in the laboratory to record parasitoid emergence. Parasitoid species diversity was similar in both landscape types (simple landscape: four species; complex landscape: five species). Mean percentage parasitism was significantly higher in the complex landscape than in the simple landscape (13.1% vs. 2.4%) but was not affected by the location within fields (near hedgerows vs. distant from hedgerows) in either landscape type.

Key words: armyworm; hedgerows; landscape structure; parasitism; Pseudaletia unipuncta.

INTRODUCTION

In many agroecosystems, landscape structural diversity has been greatly simplified and insect communities are dominated by pest species (Ryszkowski et al. 1993). Numerous studies have shown that increasing structural diversity in agroecosystems results in a greater diversity of both pest and beneficial insects, and often less damage by pests (Risch et al. 1983, van Emden 1990). This is true within fields (as the result of intercropping [Perrin 1977, Altieri et al. 1978, Risch 1980, Theunissen and Den Ouden 1980, Tukahirwa and Coaker 1982, Letourneau 1986, 1987, Vandermeer 1986, Coll and Bottrell 1994], underplanting field crops with groundcover [Ryan et al. 1980, McKinlay 1985], and promoting a weedy background [Root 1973, Smith 1976*a, b,* Altieri et al. 1977, Altieri and Whitcomb 1979, Foster and Ruesink 1984]), and at a larger between-field scale (Altieri and Todd 1981, Sotherton 1984, 1985, Coombes and Sotherton 1986, Graveson and Toft 1987, Duelli et al. 1990, Ryszkowski and Karg

1991, Ryszkowski et al. 1993). The increase in insect diversity with increasing structural diversity appears to result from two correlated factors: (1) increased plant species diversity and (2) increased plant architectural complexity (sensu Lawton 1983). More architecturally complex plant communities (e.g., adults vs. seedlings; late successional shrubs and trees vs. early successional annual herbs) have more species of insects living on them (Murdoch et al. 1972, Lawton and Schröder 1977, Lawton 1978, Southwood et al. 1979, Stinson and Brown 1983, Cornell 1986, Hawkins and Lawton 1987, Brown 1991).

Parasitoids in particular respond strongly to increasing plant architectural complexity. Hawkins and Lawton (1987) have shown that parasitoid diversity is lowest on monocots and herbs and highest on shrubs and trees. They suggest, as did Askew (1980), that trees and shrubs may have higher parasitoid diversity because they have more species of herbivores that serve as alternative hosts and attract more polyphagous parasitoids. It is also well known that the adults of many species of parasitoids exploit plants for food using nectar or secretions from aphids or scale insects (van Emden 1963, 1990, Jervis et al. 1993). Later successional habitats may, therefore, also provide more abundant

adult food resources than early successional habitats. This suggests that within agricultural fields the diversity of parasitoids and the intensity of parasitism may be greater at field edges where crops are adjacent to later-successional plant communities than in field interiors or along field edges with crop–crop or crop–early successional interfaces. Also, at a larger spatial scale, the diversity of parasitoids and the intensity of parasitism should be greater in agricultural landscapes embedded in a matrix of later-successional plant communities (old fields, hedgerows, woodlots) than in simple agricultural landscapes composed primarily of field crops. Therefore, at both the small within-field and the large between-field scales, a highly diverse landscape structure may provide the greatest potential for the biological suppression of pests by their natural enemies.

To determine if the complexity of agricultural landscape structure influences larval parasitoid species richness and overall larval percentage parasitism, we conducted field studies using the armyworm, *Pseudaletia unipuncta* (Haworth) as a host. Armyworm was chosen because it has a diverse and well-studied parasitoid complex, including 35 species of potential parasitoids in the Great Lakes Region (Muesbeck et al. 1951, Guppy 1967, Krombein et al. 1979). The armyworm is easily reared and has been previously used as a sentinel species to study parasitoid communities (Mulder and Showers 1986).

We examined the impact of structural diversity at two spatial scales. First, within fields we compared parasitoid communities on *P. unipuncta* in maize (*Zea mays* L.), near and distant from a hedgerow edge. We defined a hedgerow as an unmanaged row of trees or shrubs enclosing or separating fields (Forman and Baudry 1984). Second, we replicated these studies within a complex landscape (agricultural fields of small size embedded in a landscape of abundant hedgerows and woodlots) vs. a simple landscape (agricultural fields of large size embedded in a landscape with few hedgerows and woodlots) to determine the influence of overall landscape diversity on larval parasitoid communities. We hypothesized that: (1) overall parasitism and species richness would be lower in the interior of fields distant from hedgerows relative to the edge of fields bordered by hedgerows, (2) between landscapes, parasitism and species richness would be higher in the complex landscape than in the simple landscape, and (3) the effect of hedgerows on parasitism and species richness would be greater in the simple landscape than in the complex landscape.

METHODS

Landscape characterization

A 3.2 × 12.9 km area in Onondaga Township, Ingham County, Michigan, USA (42°25′30″ N, 84°29′00″ W) was selected for this study. The area encompassed a gradient between two different agricultural landscapes typical of southern Michigan. Our initial observation was that the southernmost 3.2 × 3.2 km is a highly heterogeneous (hereafter termed "complex") agricultural landscape whereas the northernmost 3.2 × 3.2 km is a more homogeneous ("simple") agricultural landscape. The central 6.5 km is transitional. We quantified and characterized this initial observation through an analysis of aerial photographs and digital landuse data. Black and white air photos (1:2000) taken on 12 June 1988 were obtained from the Michigan Department of Natural Resources (Lansing, Michigan, USA). Each photo was scanned at 150 dpi (dots per inch) and the resulting image transferred into ERDAS (Earth Resources Data Analysis System) 7.5 (ERDAS, Atlanta, Georgia, USA). All agricultural fields within the entire study area were identified, with 30 "complex" fields from the north and 30 "simple" fields from the south selected at random for further analysis. Using ERDAS, the following attributes of each field were measured: area, perimeter, maximum distance from a field edge, wooded perimeter per hectare of field area, number of edges and edge type per field, area to perimeter index, and the length per field of each of the following types of field edges: woodland, shrubland, wide hedgerows (>10 m), narrow hedgerows (5–10 m), herbaceous old field, herbaceous roadside, crop and residential. Analysis of differences between landscape types was conducted using *t* tests with significance levels corrected using a sequential Bonferroni adjustment (Holm 1979, Rice 1988). Digital land-use data from the Michigan Department of Natural Resources's, Michigan Resource Inventory System (MIRIS) were used to classify land use at a multi-field scale within each of the two study areas. The categories of "cropland" and "deciduous" accounted for >70% of the total land cover/use in these agricultural landscapes. The percentages of each of these land cover/use categories in the simple and complex landscapes were contrasted to give an overall assessment of land use patterns.

Armyworm parasitism

Three maize fields in the simple and three in the complex landscape, each having at least one side bordered by a hedgerow containing trees, were chosen for the armyworm parasitism study. In both the simple and complex sites, two of the hedgerows ran east–west and one hedgerow ran north–south. We chose hedgerows running in different directions in both sites to reduce the effect of prevailing southwesterly winds on parasitoid movement. We could not, however, reduce the confounding effect of field size on wind speed, which may influence parasitoid movement, because the simple landscape was by definition more open and had larger fields than the complex landscape. Also, we could not replicate simple and complex landscapes because of the labor-intensive nature of this study. Therefore, our conclusions regarding landscape influences on parasitism are limited to the areas under study.

Within each maize field, three parallel transects perpendicular to the same hedgerow and separated from one another by 25 m were set out at the center of the hedgerow. Armyworm release sites were established at 5 m and 90 m along each transect (six sites per field: three edge and three interior). The distance of 90 m from a hedgerow was chosen because this was the distance from the hedgerow to the center of the smallest field.

Armyworm larvae obtained from a laboratory colony were released onto maize plants at a time corresponding to natural armyworm activity. Larvae were released, one insect per maize plant, on three rows of healthy plants on three different dates, using a new set of plants for each release. The first (17 June) and second (24 June) releases consisted primarily of third instars and very few (<1%) second instars. The third release (30 June) consisted primarily of fifth instars and very few (<1%) fourth instars. Two age classes of armyworm larvae were released in order to maximize parasitoid diversity (Guppy 1967). The number released per site was 84 armyworms in the first release (3000 total), 42 armyworms in the second release (1500 total) and 42 armyworms in the third release (1050 total). Because we had insufficient fifth instars for the third release, armyworms were released at only two edge and two interior sites per field, except in one field, where armyworms were released at three edge and three interior sites. The first release had twice as many larvae as the second release because we had originally planned to let half the larvae mature into late fifth instars before recovering them. However, because of heavy rainfall after the first release and high larval mortality, all larvae were collected.

Larvae from the first, second, and third releases were recovered on 22 June, 28 June, and 5 July, respectively. Maize plants in the release sites were thoroughly inspected, with all recovered larvae placed individually into labeled 30-mL cups containing 10 mL of artificial diet. Because there was no evidence of armyworm infestation outside our study plots, we assumed that all larvae captured were from our releases. Larvae were returned to the laboratory and reared at 26°C, 60% relative humidity, and a 16:8 h light:dark cycle. Larvae were observed at least weekly to record stage of development, disease status, and parasite or moth emergence. Parasitoids that emerged were identified by larval and cocoon remains (Guppy and Miller 1970) and by adult characteristics. A subsample of 100 larval and pupal *Pseudaletia unipuncta* that died from disease were dissected to determine parasitism levels.

Results were analyzed using a split split-plot ANOVA design with fixed effects. In a split split-plot design there are two levels of randomization restrictions. In this study, the first restriction was applied to landscape type (complex vs. simple) and the second was applied to position within fields (near a hedgerow vs. distant from a hedgerow). Percentage parasitism was the dependent variable. Effects of the independent variables, Position and Field × Position, were tested with the Field × Position × Replicate mean square as the denominator of the F ratio. Remaining terms were tested with residual error. The percentage parasitism results could not be normalized using standard transformations because a number of sites had no parasitism. The data were instead rank-transformed prior to analysis (Conover and Iman 1981). A rank transformation obscures the magnitude of difference between treatment effects, but is effective in identifying trends in the data. Parasitoid species diversity was low; consequently, species diversity indices were not used.

Characterization of hedgerows

The structure of the six hedgerows adjacent to armyworm release sites was characterized by measuring the canopy width, canopy height, and tree and shrub species composition using a point transect method (Bonham 1989). For each hedgerow, a 100-m transect was set out adjacent to the edge sites. Using a tape measure and a clinometer, at 10, 30, 50, 70, and 90 m along the transect we measured the width and height of the canopy and identified the trees and shrubs in a second transect across the hedgerow.

RESULTS

Landscape classification

In these agricultural landscapes, combining the land cover/use categories of "cropland" and "deciduous" accounted for 74% and 83% of the total area in the complex and simple landscapes, respectively. The simple landscape contained somewhat more cropland then the complex landscape (71.4% vs. 59.4%) and slightly less deciduous habitat (11.2% vs. 14.3%). The remaining three categories of "urban," "nonforested," "water and wetlands" made up the remainder of the land cover/uses and were distributed nearly equally between the two landscapes.

There were significant differences in key structural features at the field level between the simple and complex landscapes. The complex landscape contained more fields of smaller average size with less perimeter per unit area and a shorter maximum distance to a field edge (Table 1). Fields in the complex landscape had significantly more perimeter of wooded field edge (woods, shrub and hedgerow) per hectare of field area than those in the simple landscape (Table 1). There were no significant differences in the mean number of edges per field, the mean number of edge types per field, or area to perimeter index (Table 1). With respect to the percentage of field perimeter comprised by each edge type, wide hedgerows were significantly more prevalent in the complex landscape, while fields with herbaceous roadsides and crop-to-crop interfaces were more prevalent in the simple landscape (Fig. 1).

TABLE 1. Structural features of the simple and complex agricultural landscapes ($n = 30$) examined in Onondaga township, Ingham County, Michigan, USA. Data are means $\pm$ 1 SD. Significance levels were adjusted using the sequential Bonferroni procedure. Nonsignificant differences are identified by ''(NS).''

| | Landscape type | | | |
	Simple	Complex	t	P
Total no. of fields per 3.2 km²	61	139		
Structural feature				
Mean field size (ha)	12.4 ± 10.3	3.4 ± 3.1	4.62	<0.0001
Mean field perimeter (m)	1638 ± 720	776 ± 303	6.04	<0.0001
Max. distance to edge (m)	101 ± 54	63 ± 39	3.16	0.003
Wooded perimeter per unit of field area (m/ha)	8.7 ± 19.1	23.5 ± 24.4	−2.61	0.012
No. of edges per field	6.0 ± 2.4	5.4 ± 1.6	1.26	0.214 (NS)
No. of edge types per field	4.0 ± 1.2	3.6 ± 1.3	1.35	0.184 (NS)
Area-to-perimeter index, I*	1.4 ± 0.2	1.3 ± 0.2	1.78	0.081 (NS)

* $I = P/(2\sqrt{\pi A})$. The values of I for different field shapes are: circle $= 1.0$; square $= 1.1$; rectangle: $1 \times 2 = 1.2$, $1 \times 5 = 1.3$, $1 \times 10 = 1.9$, $1 \times 20 = 2.7$.

Armyworm parasitism

Seven primary parasitoid species were recovered, four from sites in the simple landscape and five from the complex landscape (Table 2). In both the simple and complex landscapes, four species of parasitoids were recovered from sites near hedgerows and from sites distant from hedgerows (Table 2). Mean percentage parasitism was significantly higher in the complex landscape than in the simple landscape (landscape type effect) (13.1% vs. 2.4%, respectively) and varied significantly within fields (replicate within fields effect), but was not affected by position within fields (near hedgerows vs. distant from hedgerows) (Table 3; Fig. 2). Most of the parasitism was by the native braconid *Meteoris communis* (Cresson) (46.2% in the simple and 93.3% in the complex landscape). None of the 100 diseased or dead armyworm larvae/pupae dissected was parasitized.

Characterization of hedgerows

The canopy structure and tree species composition of hedgerows in the complex and simple landscapes were similar. Hedgerows in the complex landscape were wider (simple: 26.5 ± 2.4 m, $n = 15$ hedgerows; complex: 49.1 ± 4.6 m, $n = 14$ hedgerows; $t = 4.41$, $P < 0.0001$), but did not differ in height from hedgerows in the simple landscape (simple: 25.2 ± 3.8 m, $n = 15$ hedgerows; complex: 33.0 ± 4.2 m, $n = 15$ hedgerows; $t = 1.37$, $P = 0.8524$) (all are mean ± 1 SE). Both landscapes had hedgerows containing native mature trees (e.g., *Prunus serotina*, *Tilia americana*, and *Quercus alba*) and early successional trees and
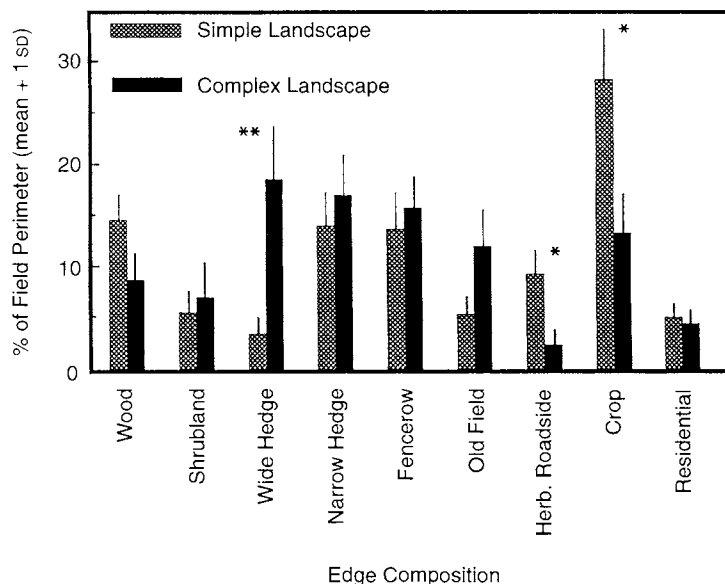

FIG. 1. Percentage of field perimeter made up of different edge types; the edge composition given is for two landscape types: three fields in ''complex'' and three fields in ''simple'' agricultural landscapes in Onondaga township, Ingham County, Michigan, USA. *$P < 0.05$; **$P < 0.01$.

TABLE 2. Primary parasitoids recovered from *Pseudaletia unipuncta* larvae released in structurally simple and complex agricultural landscapes, Ingham County, Michigan, USA.

Order: Family	Species	Landscape type			
		Complex		Simple	
		Edge	Interior	Edge	Interior
		No. of larvae parasitized			
Hymenoptera: Braconidae	*Meteorus communis* (Cresson)	68	60	2	10
Hymenoptera: Braconidae	*Glyptapanteles militaris* (Walsh)	3	2	9	4
Hymenoptera: Braconidae	*Diclogaster auripes* (Provancher)	2	⋯	⋯	⋯
Hymenoptera: Ichneumonidae	*Nepiera marginata* (Provancher)	⋯	⋯	1	⋯
Hymenoptera: Ichneumonidae	*Therion sassacus* Viereck	⋯	⋯	⋯	1
Diptera: Tachinidae	*Periscepsia helymus* (Walker)	1	⋯	⋯	⋯
Diptera: Tachinidae	Unidentified*	⋯	1	⋯	⋯

* One single large puparium; the individual died prior to emergence.

shrubs (e.g., *Crataegus* spp., *Prunus virginiana, Alnus* spp.). Also, both landscapes contained hedgerows with mixtures of mature trees and shrubs (Table 4).

DISCUSSION

The results of this study did not support our initial hypothesis that, within a landscape, overall parasitism and species richness would be lowest distant from hedgerows and greatest near hedgerows. Parasitoid species diversity was too low to draw any general conclusions regarding differences in species diversity between field edges near hedgerows and field interiors distant from hedgerows. The number of primary parasitoid species recovered in this study was similar to the number found in previous studies (Breeland 1958, Pond 1960, Guppy 1967, Untung 1978, McNeil and Turgeon 1988). However, in contrast to these previous studies, the parasitoid complex we observed was notably impoverished in regards to Diptera. This is undoubtedly a result of our choice not to concentrate effort on the more difficult-to-recover fifth and sixth instars, which are the host stages attacked by most dipterous parasitoids of armyworm (Guppy 1967).

It is unclear why overall parasitism rates did not differ between sites near and distant from hedgerows and why the degree of contrast in parasitism and species richness between sites near and distant from hedgerows was not higher in the simple landscape than in the complex landscape. Most studies examining the influence of non-cultivated borderland on predatory arthro-

pods in agroecosystems have shown that the number of predators is higher near field edges vs. field interiors (van Emden 1965a, Altieri and Todd 1981, Sotherton 1984, 1985, Coombes and Sotherton 1986), although there are some exceptions (e.g., Pollard 1971). Our results may differ because (1) parasitoids may generally have greater vagility than predatory arthropods, and (2) *Meteoris communis,* the main parasitoid in this study, may not be especially associated with hedgerow edges, but be dispersed throughout maize fields.

The first explanation can only be dealt with by exploring non-migratory movements of parasitic Hymenoptera in more detail. For example, Corbett and Plant (1993) have demonstrated the importance of the interaction between mobility and agroecosystem diversification in a simple diffusion model in which they show that interplanted vegetation can act as either a sink or a source of natural enemies depending on the mobility of the natural enemy and the specifics of agroecosystem design. The second explanation is unlikely because, in contrast to field edges, maize fields provide relatively few alternative hosts and fewer potential adult food resources (e.g., nectar and aphid honeydew; Lewis 1969a, b, Foster and Ruesink 1984). The microenvironment (high temperatures, low humidity, etc.) is also harsher in maize fields than in hedgerows at this time of year (L. Dyer and D. Landis, *unpublished data*). Previous studies of parasitoids have indicated that microclimatic factors are a potentially important influence

TABLE 3. Influence of landscape type (complex vs. simple), field, replicate (Rep.) within fields and postion within fields (5 m vs. 90 m from hedgerow edge) on the percentage parasitism of *Pseudaletia unipuncta.* ANOVA: Position and Field × Position effects were tested with Field × Position × Replicate mean square. Remaining terms were tested with residual error.

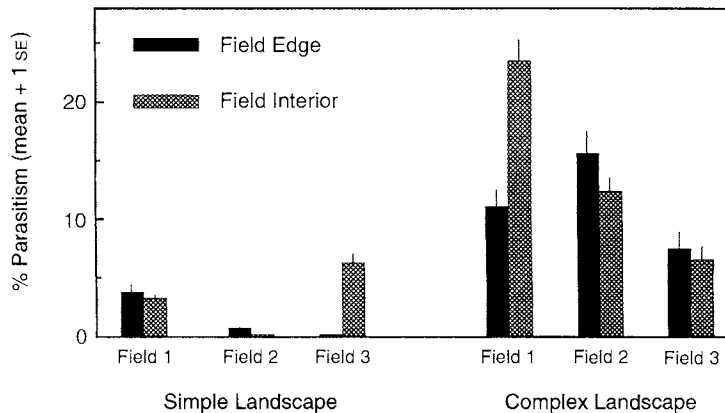| Source of variation	df	SS	MS	F	P
Landscape type	1	5149.7	5149.7	11.91	0.001
Field(type)	4	1919.3	959.7	2.22	0.1164
Rep.(Field)	6	11094.6	1849.1	4.28	0.001
Position	1	607.6	607.6	2.75	0.1482
Field × Position	1	1057.3	528.7	2.39	0.1720
Field × Position × Rep.	2	1324.7	220.7	0.51	0.7984
Error	69	29844.3	432.5	⋯	⋯

FIG. 2.   Mean percentage parasitism of *Pseudaletia unipuncta* 5 m from a hedgerow ("field edge") and 90 m from a hedgerow ("field interior") in simple and complex agricultural landscapes in southern Michigan.

on parasitoid distribution within agricultural fields (van Emden 1963, 1965, Landis and Haas 1992).

The results do, however, support our hypothesis that percentage parasitism would be greatest in the complex landscape. *M. communis* was by far the most abundant parasitoid attacking armyworm larvae, and the presence of alternative hosts in the complex landscape may explain its increased abundance. Excluding *Dargida procinata*, which does not occur in Michigan, all the alternative hosts of *M. communis* are exposed larvae that feed primarily on trees and shrubs (Krombein et al. 1979, Covell 1984, Stehr 1987, West and Miller 1989; Table 5). Of the two alternative hosts not found on trees and shrubs (black cutworm [*Agrotis ipsilon*] and alfalfa looper [*Autographa californica*]), only the black cutworm is common in maize fields. Most of the common tree and shrub species in southern Michigan agricultural hedgerows and woodlots are host plants of one or more of the alternative insect hosts of *M. com-*

TABLE 4.   Frequency of tree and shrub species in hedgerows bordering maize fields in complex and simple agricultural landscapes. Frequency is the proportion of the sample (*n* = 15 hedgerows) in which a species was present in wooded hedgerows within each landscape type.

	Landscape type	
Species	Complex	Simple
	Frequency	
Juglans nigra	0.60	···
Ulmus rubra	0.53	0.53
Prunus serotina	0.53	···
Rhus copallinum	0.40	···
Crataegus spp.	0.20	0.13
Fraxinus americana	0.20	···
Alnus spp.	0.20	···
Tilia americana	0.13	0.40
Quercus alba	0.07	0.33
Cornus spp.	0.07	0.07
Prunus virginiana	···	0.27
Acer saccharum	···	0.27
Gleditsia triachanthos	···	0.13
Morus rubra	···	0.07
Pyrus malus	···	0.07

munis. In particular, *Prunus* species (*P. serotina* and *P. virginiana*), which are a frequent component of hedgerows in the complex landscape we sampled, are hosts for five of the seven alternative insect hosts of *M. communis*.

On the other hand, *Glyptapanteles militaris*, the second most abundant parasitoid found in our study and the species that tended to be more common in the simple than in the complex agricultural landscape, is primarily a parasitoid of noctuids in herbaceous habitats. Moreover, it has several alternative hosts that occur in maize, including the cutworms *Euoxa auxilaris*, *Feltia ducens*, and *Peridroma saucia*, the armyworms *Spodoptera exigia*, *S. frugiperda*, and *S. ornithogalli*, and the corn earworm *Helicoverpa zea*. Although too few *G. militaris* were reared from the armyworms to come to a firm conclusion, the preference of *G. militaris* for herbaceous habitats and the abundance of alternative insect hosts in maize may account for more *G. militaris* being reared from armyworms in the simple than the complex habitat.

Nectar sources and moderated microclimates, both of which are likely more abundant in the complex landscape, may have also influenced parasitoid abundance. Visiting flowers to feed is a widespread habit among

TABLE 5.   Reported alternative hosts for *Meteoris communis*.

Family	Species
Noctuidae	*Amphipyra pyramidoides* Guenée
	Orthosia hibisi (Guenée)
	Orthosia revicta (Morrison)
	Dargida procincta (Grote)
	Lithophane laticinerea (Grote)
	Lithophane bethunei (Grote and Robinson)
	Eupsilia sidus (Guenée)
	Autographa californica (Speyer)
	Peridroma saucia (Hubner)
	Agrotis ipsilon (Hufnagel)
	Xylena nupera (Lintner)
Lymantriidae	*Malacosoma americanum* (F.)
Tortricidae	*Grapholitha* sp.

parasitoids, and it is widely accepted that individual parasitoids commute between insect-host-containing and plant-food-containing areas (Powell 1986, Jervis et al. 1993). In our study the complex landscape with its smaller fields and more abundant wooded and shrubby "edge" habitat should have had more abundant nectar resources closer to field interiors than the simple landscape. This may contribute to the higher rates of parasitism observed in the complex landscape. Also, the complex landscape, with a greater percentage of its area in hedgerow and other wooded habitats, may have provided more abundant favorable microhabitats for parasitoids (van Emden 1965a, Lewis 1969a, b).

Alternatively, the gradient of parasitoid density may have been unrelated to landscape complexity, or there may have been other environmental differences underlying land use patterns that affected parasitoid density. Because the simple and complex sites were only 6.5 km apart, we feel that a north–south gradient alone is very unlikely to explain the magnitude of difference in rates of parasitism that were evident in this study. Although differences in land use patterns between the complex and simple landscapes do reflect differences in topography and soil profile (the complex landscape is slightly hillier, with more wet areas), these differences are relatively small and indeed form the basis for succeeding anthropogenic influences on landscape complexity. Future studies should explore the generality of the relationship between landscape complexity and rates of parasitism by replicating studies such as ours among additional complex and simple agricultural landscapes.

While the pattern of increased parasitism of an herbivore in a complex landscape has been demonstrated, more research is needed to determine the specific mechanisms of this effect and to explore generalizations to other herbivore species. At the mechanistic level, studies examining the phenology of *M. communis* in Michigan and interactions with specific alternative hosts are needed. Determination of the realized host range (Shaw 1994) in these specific landscapes is critical. Determination of the adult food and microclimate requirements of *M. communis* may also be revealing (Landis and Haas 1992).

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