

Response of generalist and specialist insect herbivores to landscape spatial structure

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Abstract

The purpose of this study was to investigate the effect of changes in landscape pattern on generalist and specialist insects. We did this by comparing the species richness and abundance of generalist and specialist herbivorous insects in alfalfa (*Medicago sativa*, L.) fields on 26 agricultural landscapes that differed in spatial structure. The insects were from the families Curculionidae (Coleoptera), weevils, and Cicadellidae (Auchenorrhyncha), leafhoppers.

We hypothesized that: (1) generalist richness and abundance would be highest in landscapes with high diversity (Shannon-Wiener); (2) specialist richness and abundance would be highest in landscapes with (i) high percent cover alfalfa and (ii) low mean inter-patch distance. We tested for these effects after controlling for the patch-level effects of field size, field age, frequency of disturbance and vegetation texture.

The important findings of the study are: (1) generalist richness and abundance increased with increasing landscape diversity and (2) isolation (percent cover alfalfa in the landscape and/or mean inter-patch distance) does not affect specialist insects. These results are significant because they indicate that both generalist and specialist insects may move over much larger distances than previously thought. This is one of the first studies to demonstrate a large scale effect of spatial structure on insects across a broad range of landscapes.

Introduction

An important concept in landscape ecology is that environments are comprised of a heterogeneous mix of habitat patches, where habitat patches are discrete areas in which an organism obtains resources and/or breeds (Fahrig and Merriam 1994). The pattern of habitat patches on the landscape changes over time. The landscape has a dynamic spatial structure. This structure can influence the persistence of both local and regional populations of organisms.

In order for regional populations to survive, local extinctions must be balanced by (re)colo-

nizations of habitat patches (Fahrig and Merriam 1994; Hanski 1994) via dispersal of organisms over the landscape. Changes in landscape structure, such as the reduction of the proportion of one or more patch types or the increase in patch isolation, will alter the ability of organisms to disperse (Merriam 1984; Fahrig and Merriam 1985). Species that can not disperse effectively as a result of a change in structure will suffer reductions in regional population sizes (Fahrig and Merriam 1994).

The purpose of this study was to investigate the effect of landscape pattern on generalist and specialist insects. We accomplished this by compar-

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ing the species richness and abundance of generalist and specialist herbivorous insects in alfalfa (*Medicago sativa*, L.) fields in several agricultural landscapes that differed in both proportion of alfalfa and diversity (Shannon-Wiener) of habitat types. The selected insects were from two families, Curculionidae (Coleoptera) and Cicadellidae (Auchenorrhyncha).

Different species respond to their environment at different spatial and temporal scales (e.g., Wiens and Milne 1989; With 1994a,b). However, since agricultural fields are internally homogeneous and large anthropogenic disturbances generally occur at the scale of the field (1–10 ha), we expect that many if not most insects in farmland will respond to pattern at this scale. Given the large effects of human activities on landscapes, it is important to determine whether there are any responses of insects to these activities at this spatial scale. This study is one of the first to relate insect species richness and abundance to large-scale spatial pattern across a range of landscapes (also see Ryszkowski *et al.* 1993; Marino and Landis 1996).

We hypothesized that if there were any large-scale effects of spatial pattern on insect herbivores in agricultural landscapes then: (1) generalist species richness and abundance would increase as landscape diversity increased and (2) alfalfa specialist species richness and abundance would increase as isolation decreased. For the latter hypothesis we used two measures of isolation: the percent cover alfalfa and the mean inter-patch distance between alfalfa fields. We predicted that specialist species richness and abundance would (1) increase as percent cover of alfalfa in the landscape increased and (2) would decrease as the mean inter-patch distance increased.

An increase in the diversity (sensu O'Neill *et al.* 1988) of a landscape means that the number of different habitat types increases and/or the proportions of the habitat types present become more equal. This represents a potential increase in the habitat available for use by generalist insect populations, since generalists may supplement (Dunning *et al.* 1992) their resources by utilizing more than one habitat type. When the number of habitat types on a landscape that can be used by a generalist species increases, patch isolation decreases

and connectivity becomes greater (Taylor *et al.* 1993). This means dispersal rates will increase and the rate of local extinctions will decrease due to increased immigration (Brown and Kodric-Brown 1977). Faster recolonization of local extinctions will also occur due to increased dispersal rates (Fahrig and Merriam 1985). These two effects lead to an increase in the species richness and abundance of generalist insects at the landscape level (Hanski 1994).

An increase in the proportion of alfalfa on the landscape should result in either larger or more alfalfa specialist populations (or both). In either case, persistence of a population at the landscape-level should be increased since: (1) larger populations will be less susceptible to extinctions via demographic fluctuations than smaller populations (Lande 1988; 1993) and (2) a higher number of local populations should ensure that not all local populations will go extinct at the same time.

Reductions of alfalfa patch isolation distances may lead to higher connectivity for specialist insects dispersing over the landscape. Increased connectivity will lead to more dispersal which will result in fewer local extinctions and/or faster recolonization of local extinctions (Brown and Kodric-Brown 1977). This, coupled with the effect(s) of increased proportion of alfalfa in the landscape, should lead to increased specialist species richness and abundance at the landscape level.

Based on results from simulation models of spatially structured populations, there appear to be nearly consistent effects of spatial and temporal patch structure on local population sizes (e.g., Kareiva 1990; Hastings 1991; Fahrig 1992; Hanski 1994; Watkinson and Sutherland 1995). Specifically, population size is predicted to increase with increasing patch size and patch age and to decrease with increasing frequency of disturbance. These three aspects of habitat patch structure have been shown to influence insect population size (McLain and Shure 1990; Harrison and Thomas 1991; Weisz *et al.* 1994). In addition, numerous studies have demonstrated the importance of within-patch vegetation texture to herbivorous insects (e.g., Tahvanainen and Root 1972; Root 1973; Cromartie 1981; Bach 1980; Evans 1983; Kareiva 1983; Coll and Bottrell 1994). For example, the density and species diversity of the vegetation can






-  Zone 1 - Woodland, pasture and hay systems
-  Zone 2 - Pasture, hay and mixed systems
-  Zone 3 - Corn and corn/grain monoculture systems

Fig. 1. Map of study area showing position of the 26 landscapes (white and black circles) along with the regional-scale pattern of agricultural intensity. The agricultural intensity zones 1-3 were derived from smaller-scale agricultural land use intensity maps of the Regional Municipality of Ottawa-Carleton (RMOC). The farming systems in the legend and described in the text are based on the land use intensity categories obtained from the RMOC maps.

influence herbivore movement (Kareiva 1983) and alter the vulnerability of the herbivore to attack from natural enemies (Coll and Bottrell 1994).

We tested the landscape-level hypotheses after controlling for any effects of the patch-level variables: age, size and frequency of disturbance. For generalist herbivores we also controlled for within-patch vegetation diversity. For specialist herbivores we also controlled for within-patch proportion of legumes (alfalfa plus clover).

Methods

Study area

We selected 26 landscapes containing alfalfa fields, spread over a 1200 km² area in the south-eastern portion of the Ottawa-Carleton Region, Ontario, Canada (Fig. 1). We selected alfalfa fields in landscapes that varied in both diversity of habitat types and percent cover of alfalfa. The clumped distribution of landscapes shown in Fig. 1 arose because (i) many alfalfa fields could not be sam-

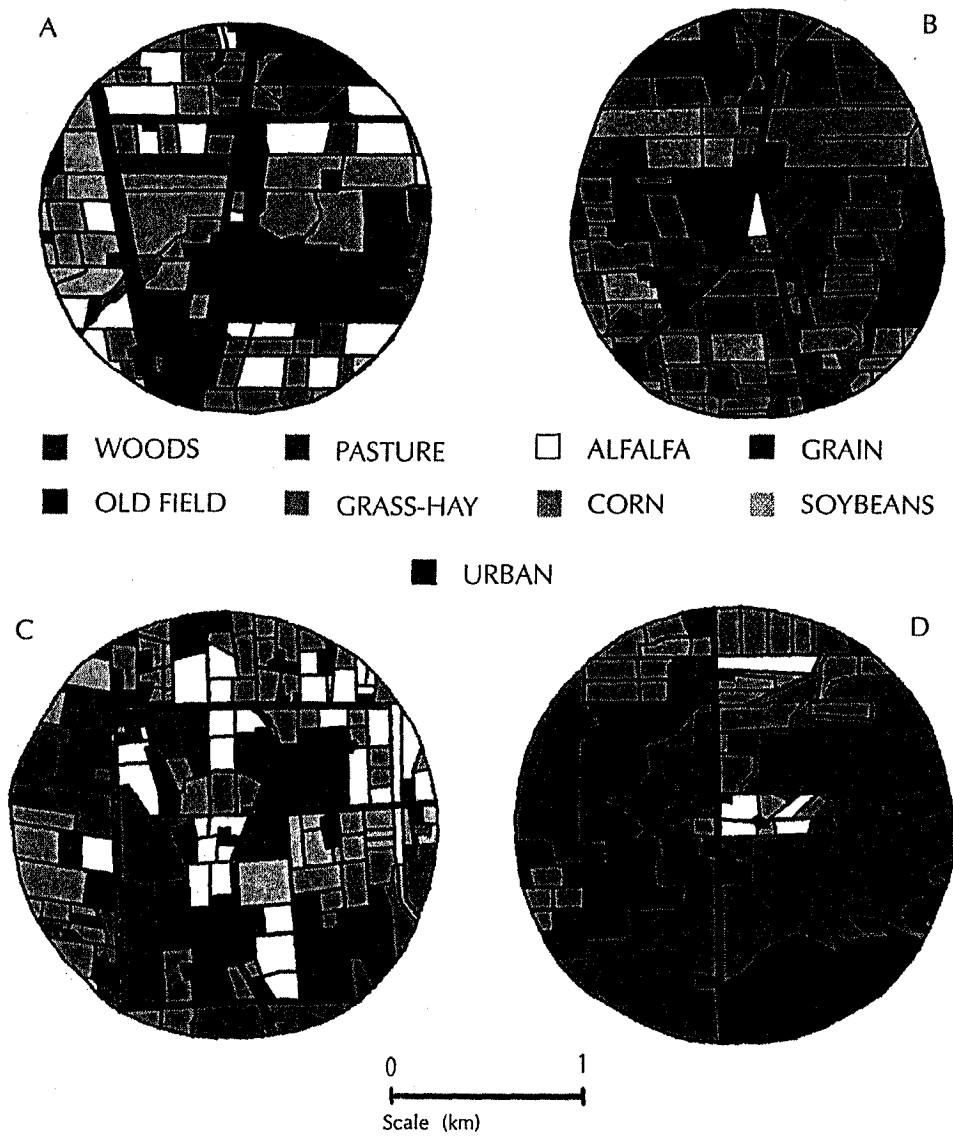


Fig. 2. Examples of high and low *alfcover* and high and low *landscape diversity*. Landscapes A and B show high and low *alfcover*, respectively. Landscape A has a value of 12.61% and landscape B has a value of 0.64%. Landscape C and D show high and low *landscape diversity*, respectively. Landscape C has $H' = 2.13$ and landscape D has $H' = 1.44$. Note: there was no significant correlation between *landscape diversity* and *alfsol* in the 26 landscapes studied.

pled due to lack of consent from landowners; (ii) some areas within the study region contained few, if any, alfalfa fields and therefore no landscapes were chosen in these areas; and (iii) time constraints required that we minimize the amount of driving between landscapes.

The study region shown in Fig. 1 contains three broad agricultural land use intensity zones. Zone

1 is dominated by woodland, and a few pasture-hay systems located on the periphery of the Marlborough Forest in the southwest. The soils are mainly shallow and undifferentiated over limestone bedrock. The pasture and hay systems are characterized by grass-hay, alfalfa and pasture grown in rotation on small- to medium-sized fields. Fertilizer and labour inputs are very low.

Table 1. Life history attributes of weevil and leafhopper species included in analyses.

	Life history attributes		
	# Generations/yr	Vagility	Preferred host plants
Generalists			
Weevils			
<i>Ceutorhyncus floralis</i>	na	na	broad-leaved plants
<i>C. erysimi</i>	na	na	broad-leaved plants
<i>C. sp.</i>	na	na	broad-leaved plants
<i>Rhinoncus castor</i>	na	na	broad-leaved plants
Leafhoppers			
<i>Aceratagllia sp.</i>	1	na	broad-leaved plants
<i>Aphrodes sp.</i>	1	na	broad-leaved plants
<i>Macrosteles quadrilineata</i>	1	na	broad-leaved plants and grasses
Specialists			
Weevils			
<i>Hypera postica</i>	1	medium	clovers and alfalfa
<i>H. nigrirostris</i>	1	low	clovers and alfalfa
<i>Sitona flavescens</i>	1	na	legumes
<i>S. hispidulus</i>	1	medium	clovers, alfalfa, trefoil
<i>S. lineellus</i>	1	na	legumes
<i>Tychius picirostris</i>	1	low	clovers and alfalfa
<i>T. stephensi</i>	1	na	red clover and alfalfa
Leafhoppers			
<i>Empoasca fabae</i>	1*	high	legumes**

*Does not overwinter in Ontario;

**Only known host plants in Ottawa region.

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Zone 2 is dominated by low to medium intensity agriculture where pasture, hay and mixed systems are interspersed along with some medium-sized wooded areas. The soils vary from clay-loams to sands. The mixed system is characterized by corn, cereal grain, hay, alfalfa and pasture in rotation on

medium-sized fields. Fertilizers are commonly used and labour inputs are moderate. Zone 3 is dominated by medium to high intensity agriculture where corn and corn/grain monoculture systems are mixed together. The soils are mainly clay-loams and loams. The corn system is character-

ized by corn, cereal grain, hay and pasture grown in rotation on medium- to large-sized fields. Large, mechanized dairy operations are common and fertilizer application is universal. The monoculture system is characterized by continuous cultivation of corn or cereal grain without rotation on large fields. Fertilizer application rates are high but labour inputs tend to be low. Sampled alfalfa fields located within Zone 3 were on mixed system landscapes only.

Each landscape consisted of a field of alfalfa in the centre of the landscape, surrounded by other agricultural fields and "natural" habitat patches such as woods and old fields. The landscapes measured 1 km in radius from the sample field edge. This arbitrary size created a landscape within which all fields and habitat patches could be identified during the sampling season. Landscapes with high diversity were composed of a variety of agricultural crops and old fields along with some remnant patches of forest (Fig. 2). Landscapes with low diversity generally contained fewer types of agricultural crops with alfalfa, grass-hay and pasture being the most common. These landscapes also had higher proportions of forest and old fields. Landscapes with high or low percent cover of alfalfa varied greatly in both the number and type of other habitats (Fig. 2).

Sampling technique

Each alfalfa field was sampled once a week for 11 weeks from 2 June to 16 August, 1994. Each field was sampled by walking a 40 m transect in the approximate field centre and sweeping a flight net through the vegetation at each pace. A 1 m² quadrat was randomly placed near the start and end of each transect and the percent cover of alfalfa, clover, grass, other dicot plants and bare ground were estimated. We also recorded the number of times the sampled fields were cut over the season and the number of years since initial alfalfa planting. We only sampled at the field centre due to time constraints.

Leafhoppers (Auchenorrhyncha: Cicadellidae) and weevils (Coleoptera: Curculionidae) were separated from all other insects collected. The leafhoppers were identified to species using Beirne

(1956), Borror *et al.* (1993), Hamilton (1983) and K.G.A. Hamilton (pers. comm.). The weevils were identified to species using Titus (1911), Arnett (1968), Clark (1971) and A. Howden (pers. comm.). When identification to species was not possible only the genus was recorded. Table 1 lists the specialist and generalist genera/species included in the analyses along with relevant life history attributes. The Ottawa-Carleton region lies close to the northern limit of the ranges of many of the insect species included in this study. Some life history attributes (*e.g.*, number of generations/year) will therefore differ from populations farther south. Life history data presented here are based on available observations of the species from the location nearest to the Ottawa-Carleton region.

The four instances where only the genus level was recorded occur in the generalist category. To our knowledge, each instance represents individuals that belong to one species within the genus reported (*e.g.*, *Aphrodes* sp. one species). Regardless, since many leafhopper species must be identified by observing the male genitalia, we cannot be entirely certain that each instance where genus alone is reported represents one species. If a genus represents more than one species in our analyses then lumping these species together will underestimate species richness within the generalist category. However, our measure of richness reflects the number of species within only two families of insects found within the sampled fields. As such, our measure is merely intended as an index of the total species richness within the fields.

Defining generalists and specialists

The classification of insect species into specialist and generalist categories was based on the food resources that each species relies on. We defined a generalist as a species that feeds on both legumes and any other plant family found within the study area. We defined a specialist as a species that feeds only on legumes during all stages of the species' development. If a species feeds on legumes and other plants but these other plants are not found in the study area, we treated the species as a specialist. All sampled fields were alfalfa; however, there were also soybean (*Glycine max*,

L.) fields in many of the landscapes. The "specialist" species *Empoasca fabae* is known to feed on both alfalfa and soybeans (along with other host plants either not found or not found in significant numbers in our study area). In the field, it is not known whether there is a preference for alfalfa over soybeans. We dealt with this by removing the effect of the percent cover of soybeans on the landscape from our analyses involving specialist insects (see statistical methods).

Quantifying landscape structure

All habitat patches within our landscapes were identified on 1:15 000 scale air photos to determine landscape composition. We drew maps of the various patch types for each landscape. The areal proportion of each patch type within a landscape was measured using a digital planimeter. The patch types included: pasture, grass-hay, alfalfa, corn, soybean, grain, old fields, woodlots and urban areas (see Fig. 2).

The Shannon-Wiener diversity index is most commonly used to measure species diversity. It can also be used to measure landscape diversity; in this case it measures the diversity of patch types within the landscape by combining the number of different patch types with their relative proportions (O'Neill *et al.* 1988).

The Shannon-Wiener diversity index (H') is:

$$H' = \sum p_i \ln p_i$$

Where H' is the landscape diversity index (LANDSCAPE DIVERSITY) and p_i is the proportion of the landscape in patch type i (Mladenoff *et al.* 1993). This index was also used to measure the within-field vegetation diversity.

Percent cover alfalfa (ALFCOVER) was measured as the total area of alfalfa contained within a landscape divided by the area of the landscape, all multiplied by 100. Isolation was also measured as the mean of the edge-to-edge distances of the sampled alfalfa field to all other alfalfa fields in each landscape (ALFISOL).

Quantifying patch structure

The three patch-level variables included in all analyses were sample field size (SIZE), sample field age (AGE) and number of times the sample field was cut over the study period (CUTS). The age of each sample field was recorded as 1 (planted the previous season), 2 (planted two years before), 3 (planted 3 years before), or 4 (planted 4 or more years before). The number of cuts a field received is a measure of the frequency of disturbance. Note that alfalfa fields in the Ottawa-Carleton region are not sprayed with pesticides and therefore cutting represents the only consistent and measurable disturbance at the field level. Since competitive exclusion may occur in fields that are disturbed infrequently (Connell 1978) or in fields that are very old, relationships between species richness or abundance and field age and cuts may not be linear. To check this we included both first and second order terms for AGE and CUTS in all six analyses.

The two analyses dealing with generalist insects also included a measure of within-field vegetation diversity (FIELD DIVERSITY). FIELD DIVERSITY was derived using the Shannon-Wiener index based on the proportion of legumes, grass, other dicots and bare ground estimated within 1 m² quadrats (see above). The four analyses dealing with specialist insects also included the within-field proportion of legumes (alfalfa and clover) (FIELD LEG).

Statistical methods

Insect abundance and species richness were summed for each field over the 11 week sampling period. Within-field proportions of legumes (alfalfa and clover), grasses, other dicots and bare ground were averaged over the sampling period. Multiple linear regressions were conducted to determine if there were effects of: (1) LANDSCAPE DIVERSITY on i) GENERALIST RICHNESS and ii) GENERALIST ABUNDANCE; (2) ALFCOVER on i) SPECIALIST RICHNESS and ii) SPECIALIST ABUNDANCE; and (3) ALFISOL on i) SPECIALIST RICHNESS and ii) SPECIALIST ABUNDANCE. The patch-level variables SIZE, AGE, AGE², CUTS and CUTS² were included in all six analyses. FIELD DIVERSITY was included in

the two generalist analyses and FIELD LEG was included in the four specialist analyses.

To deal with the problem of soybean fields (see "defining generalists and specialists") we fitted a linear model that related percent cover of soybeans in the landscape to SPECIALIST RICHNESS and used the residuals from this model as a new measure of SPECIALIST RICHNESS. We tested for effects of ALFCOVER and ALFISOL on the new measure of SPECIALIST RICHNESS. We did the same for SPECIALIST ABUNDANCE.

Diagnostic plots of the initial model for GENERALIST RICHNESS indicated that three data points (GENERALIST RICHNESS values of 4 and 5) had a disproportionately large influence on the overall fit of the model. We dealt with this by giving all fields with a GENERALIST RICHNESS equal to or greater than 3 species a value of 3. This produced a more balanced model in which no one value had a greatly increased influence on the model fit.

All models presented are ANOVA models, fitted with stepwise regression using S-plus (Chambers and Hastie 1989). By using stepwise regression we were able to test for effects of a large number of independent variables, despite having a relatively small sample size ($n=26$) (see Chambers and Hastie 1989; Venables and Ripley 1994). Where necessary, dependent variables were either log- or square root-transformed to satisfy the assumption of normality. Adequacy of fit was determined by examining quantile-quantile plots of residuals and plots of residuals versus fitted values. Actual probabilities of Type I error ($p(F)$) are reported based on Type III sums of squares.

Due to spatial overlap between eight separate groups of landscapes (see above) a lack of independence in the response variables was suspected. We determined whether this was the case by performing spatial autocorrelation analysis on the response variables. Spatial autocorrelation analysis is used to test for the presence of more similar or less similar values at pairs of locations than would be expected if the data were randomly distributed (Fortin *et al.* 1989; Legendre and Fortin 1989; Legendre 1993). Spatial autocorrelation analysis was conducted using the R Package (Legendre and Vaudor 1991). Moran's I Coefficient (Fortin *et al.* 1989; Legendre and Fortin 1989) was used to estimate the degree of spatial

autocorrelation among values for (1) GENERALIST RICHNESS, (2) GENERALIST ABUNDANCE, (3) SPECIALIST RICHNESS, and (4) SPECIALIST ABUNDANCE.

Results

There was a total of 760 generalist individuals and 1901 alfalfa specialist individuals identified to species or genus levels. There was a total of 8 generalist taxa (4 were identified to the genus level and 4 to species) and a total of 8 specialist species identified. Richness values ranged from 1 to 5 for generalists and from 1 to 6 for specialists. Note that generalist richness values only ranged from 1 to 3 in our analysis because values > 3 were set = 3 (see methods). Abundance values ranged from 2 to 94 for generalists and from 11 to 309 for specialists. Spatial autocorrelation analysis showed no significant values of Moran's I Coefficient for species richness or abundance of generalists or specialists for the overlapping landscapes. This indicates that the 26 landscapes may be regarded as independent data points in the analyses.

The number of generalist species found in alfalfa fields was most strongly influenced by habitat diversity at the landscape-level (LANDSCAPE DIVERSITY $p(F) = 0.047$). There were also marginally significant effects of frequency of disturbance (CUTS $p(F) = 0.064$) and field age (AGE $p(F) = 0.081$) (Table 2a). Generalist species richness increased with increasing landscape diversity and field age and decreased with increasing frequency of disturbance. Together, these three variables explained 35% of the variability in generalist species richness (Table 2a).

The number of generalist individuals (log-transformed) found in alfalfa fields was influenced only by landscape diversity (LANDSCAPE DIVERSITY $p(F) = 0.02$, $R^2 = 0.2$) (Table 2b.). As for GENERALIST RICHNESS, GENERALIST ABUNDANCE was higher in alfalfa fields situated in landscapes with higher diversity.

Table 3a presents results from analyses for both specialist richness hypotheses (see "statistical methods"). Since there were no effects of either ALFCOVER or ALFISOL the results are the same, therefore we present the results in a single table. The number of specialist species found in alfalfa

Table 2a. Analysis of variance table. The response variable is GENERALIST RICHNESS, measured in single alfalfa fields within 26 landscapes.

	Type III					
	Parameter Estimate	df	Mean Square	F	p(F)	R ²
CUTS	0.43	1	1.88	3.80	0.064	0.35
AGE	0.53	1	1.65	3.34	0.081	
LANDSCAPE DIVERSITY	2.02	1	2.19	4.42	0.047	
Residual		23	0.81			

Table 2b. Analysis of variance table. The response variable is the natural logarithm of GENERALIST ABUNDANCE plus one, measured in single alfalfa fields within 26 landscapes.

	Type III					
	Parameter Estimate	df	Mean Square	F	p(F)	R ²
LANDSCAPE DIVERSITY	1.78	1	2.95	5.94	0.022	0.20
Residual		24	0.50			

fields was lower in more frequently cut fields (CUTS $p(F) = 0.001$, $R^2 = 0.36$) (Table 3a). No other variables significantly influenced SPECIALIST RICHNESS.

Table 3b presents results from analyses for both SPECIALIST ABUNDANCE hypotheses (see "statistical methods"). Since there are no effects of either ALFCOVER or ALFISOL the results are the same, therefore we present the results in a single table. The number of specialist individuals (square root-transformed) found in alfalfa fields was influenced by the within-field proportion of legumes (FIELD LEG $p(F) = 0.00004$) and the number of times fields were cut (CUTS $p(F) = 0.04$) (Table 3b). The number of specialists increased as FIELD LEG increased and decreased as cuts increased. Together, FIELD LEG and CUTS explained 57% of the variability in SPECIALIST ABUNDANCE (Table 3b).

Discussion

Generalist richness and abundance

There was a significant effect of landscape diversity on both generalist species richness and generalist abundance. As we predicted, generalist

Table 3a. Analysis of variance table. The response variable is SPECIALIST RICHNESS (with effects of soybeans in the landscape removed) measured in single alfalfa fields within 26 landscapes.

	Type III					
	Parameter Estimate	df	Mean Square	F	p(F)	R ²
CUTS	1.21	1	16.83	13.72	0.001	0.36
Residual		24	1.23			

Table 3b. Analysis of variance table. The response variable is the square-root of SPECIALIST ABUNDANCE plus 0.5, (with effect of soybeans in the landscape removed) measured in single alfalfa fields within 26 landscapes.

	Type III					
	Parameter Estimate	df	Mean Square	F	p(F)	R ²
FIELD LEG	0.11	1	102.60	26.15	0.00004	0.57
CUTS	1.32	1	17.99	4.58	0.043	
Residual		23	3.93			

richness and abundance within a field increased as the number of patch types in the landscape increased and/or their proportions became more equal. Insects that utilize a variety of resources found in different types of agricultural fields may not distinguish between alfalfa fields and other fields such as grain fields or old fields. For example, the generalist leafhopper *Macrostoteles quadri-lineata* feeds on both broadleaved plants and grasses. Both of these resources may be found within alfalfa fields, grass-hay fields, old fields and even in roadside verges. The combination of a lack of effect of within-field diversity and a significant effect of landscape diversity suggests that generalist insects, at the population level, discriminate between the spatial pattern of resources at scales larger than the agricultural fields (mean alfalfa field size $66\,490.4\text{ m}^2 \pm 64\,142.6\text{ s.d.}$) in the present study. This is significant since the majority of studies to date have focussed on within-field effects of habitat pattern on insects (e.g., Root 1973; Cromartie 1975; Andow 1983; Shelton and Edwards 1983; Flinn *et al.* 1990; Coll and Bottrell 1994). The significant effects of the temporal variables field age and frequency of distur-

bance on generalist richness indicate that generalist species respond to temporal dynamics at the scale of the field (1–10 ha).

Populations of generalist insects may be able to persist in otherwise relatively unsuitable (*i.e.* sink) habitat when they can supplement (Dunning *et al.* 1992) their resources with those found in other habitat types (*e.g.*, corn and grain fields, old fields, and woodlots). In fact Andr n (1992) found that the density of hooded crows (*Corvus corone*), a habitat generalist, was greatest in landscapes that contained relatively even proportions of farmland and forest, lending support to our suggestion.

Dunning *et al.* (1992) refer to supplementation as the ability of an organism to utilize more than one habitat type within a landscape. Here we refer to supplementation as a population level process in which individuals move between fields within a landscape such that different individuals may encounter different fields. The implication is that the spatial extent of a population of generalist insects in farmland is larger than the scale of a single field. Given the present state of knowledge regarding insect movement this seems questionable. However, until only very recently it has been virtually impossible to directly determine how insects move (see Mascanzoni and Wallin 1986; Roland *et al.* 1996) in response to habitat pattern at large spatial scales. The possibility remains that individual insects do move between several resource patches (fields) over the landscape many times during their life cycle and that these cases are not exceptional. Examples of large-scale movements by insects include the long distance migratory flights of the leafhopper *Empoasca fabae* and the monarch butterfly. Neither species overwinter in Canada but migrate northwards from the south-central United States (Pienkowski and Medler 1964; DeLong 1971) and northern Mexico, respectively. These movements occur at a larger ecological scale than between-resource movements but they do provide evidence that at least some insects, both small- and large-winged, are capable of moving over very large distances during their lifespan.

The damselfly *Calopteryx maculata* can link breeding and foraging resources that are separated in space by up to about 500 m (Taylor and Merriam 1995) and flights of over a kilometer

have been observed via mark - re-observation techniques (P. Taylor pers. comm.). Additionally, the butterfly *Plebejus argus* is able to colonize nearly all habitat patches within 1 km from other populated patches (Thomas and Harrison 1992) and more than 10% of seed feeding bugs, *Lygaeus equestris*, move more than 1 km between breeding areas in successive years (Solbreck and Sillintullberg 1990).

An effort must be made to study the movement behaviour of insects, using direct observation and manipulative techniques. The spatial extent of insect movements must be examined and linked to the variety of behaviours (*e.g.*, foraging, mate seeking, predator escape, dispersal, migration) that can underly them. In this way we can begin to gain a mechanistic understanding of how organisms interact with the landscape and how these interactions may influence population dynamics.

Specialist richness and abundance

We did not find a relationship between isolation (percent cover alfalfa or mean inter-patch distance) and specialist insect richness or abundance. The lack of an effect of isolation suggests that the mean distance (480m \pm 167.13 s.d.) between sampled and other alfalfa fields are within the dispersal abilities of the specialist insects included in the present study. This is likely the case for the potato leafhopper, *E. fabae*, which, as stated earlier, does not overwinter in northern US or Canada; instead it migrates from the Gulf States each spring via prevailing wind currents (DeLong 1971). Alternatively, the mean isolation distances between sampled alfalfa fields and all other alfalfa fields may overestimate the actual distances between patches of suitable habitat for alfalfa-clover specialists. The presence of host plants in field margins and roadside verges may act as: (1) suitable breeding habitat, (2) shelter habitat for insects escaping recently disturbed fields (*e.g.*, Schaber *et al.* 1990) or (3) sources of (re)colonization for alfalfa fields.

The importance of non-crop areas, such as field margins and roadside verges, as habitat for insects is well documented (*e.g.*, Schaber *et al.* 1990; Ryszkowski *et al.* 1993). However, the resolution

at which habitat patches could be identified was constrained by the size (1 km radius) and number ($n=26$) of our landscapes. Due to the highly dynamic nature of the agricultural landscape we had to ensure that all habitat patches included in our study could be identified within one growing season (*i.e.* May to September). This reduced our ability to enumerate all habitat patches ranging from large fields down to roadside verges and field margins. Our inability to identify these small habitat types may have led to a failure to detect a landscape-level effect of habitat pattern (percent cover alfalfa and/or mean inter-patch distance) on specialist insects. Very small habitat patches may act as stepping stones that effectively increase the dispersal capabilities of a population of specialist insects. This may be especially true if the dispersal of insects in farmland is, at least to some degree, density dependent. The structure of the landscape may influence the movement behaviour of the insects which in turn can influence demography at the landscape-level.

The results of this and another study (Fahrig and Jonsen *in review*) indicate that there are some general effects of habitat spatial and temporal structure on insect assemblages. This is important when considering regional planning and management because desired effects (*i.e.* control of pest species and/or protection of rare or endangered species) can be produced at a general level. In other words, we do not necessarily have to plan to manage landscapes (or single fields) for thousands of species simultaneously. Additionally, the large-scale effect of landscape diversity on generalist insects indicates that pest management efforts must be focussed not only within the field boundary but also beyond it. Management of agricultural pests are likely to be more effective if efforts are linked over a larger spatial extent than has previously been considered.

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