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Effect of Habitat Patch Characteristics on Abundance and Diversity of Insects in an Agricultural Landscape

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ABSTRACT

The objective of this study was to test for general effects of patch size, patch isolation, disturbance frequency, and patch life span, on density and diversity of organisms. We sampled predominantly herbivorous insects in 31 alfalfa fields that varied in size, isolation, frequency of disturbance by cutting, and age (number of years planted in alfalfa). Effects on insect relative density and diversity were examined at three taxonomic levels: all insects, eight separate orders, and six legume-specialist weevil species. We found that (a) more isolated alfalfa fields had higher overall insect richness, (b) fields with higher disturbance frequency had lower overall insect richness, and (c) fields of intermediate age had highest insect richness. In some cases these patterns were reflected at lower taxonomic levels, but in many cases they were not. These results are important because they indicate that, although we cannot simultaneously tailor a landscape for each of thousands of species, we may be able to produce desired effects at a more general level.

Key words: agro-ecosystem; patch size; resource concentration hypothesis; patch isolation; metapopulation; patch age; intermediate disturbance hypothesis; insect density; insect richness.

INTRODUCTION

The view that many populations are "patchy" or spatially structured in discrete "local populations" has become increasingly prevalent in the ecological literature (Wu and Loucks 1995). A variety of models have been used to study the dynamics of such populations [for example, see Fahrig and Paloheimo (1988a), Kareiva (1990), Hastings (1991), Fahrig (1992), Hanski (1994), Hastings and Harrison (1994), and Watkinson and Sutherland (1995)]. In these models, a regional population is structured as a set of local or patch populations among which exchange of individuals occurs. This exchange reduces the probability of local extinction through a *rescue effect* (Brown and Kodric-Brown 1977) and allows recolonization of local extinctions when they do occur. Local extinction occurs through one or both of two processes. First, local stochastic events within a habitat patch may cause high mortality or low natality; these events can be generically described as *disturbances*. Second, the local habitat itself may disappear; if such disappearances occur on a short time scale relative to the generation time of the organism, the habitat is *ephemeral*. The degree to which habitat patches are ephemeral can be described in terms of patch *life span*, or the typical number of years (or other time units) that habitat patches persist.

The objective of such modeling is to make general predictions about the effects of patch characteristics on population density and survival probability, and on species richness. Patch characteristics include the spatial characteristics: patch size and patch isolation;

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and the temporal characteristics: disturbance frequency and patch life span. Modeling studies have produced a variety of predictions, depending on model assumptions. Likewise, empirical studies have produced a variety of results.

The effect of patch size on population density has been predicted to be either positive or negative. The resource concentration hypothesis (Root 1973) predicts that larger host plant patches should have larger insect densities because the probability of an insect finding a large patch is higher and the probability of an insect leaving a large patch is lower. For species with risk-spreading movement behavior, however, there may be a negative relationship between patch size and population density [for example, see Fahrig and Paloheimo (1987) and Conner and Neumeier (1995)]. In addition, a prey or host species that is strongly controlled by natural enemies can show a negative relationship between patch size and density, if the enemy's dispersal ability is low relative to that of the prey or host (Kareiva 1990; Pearman 1995; Redpath 1995).

Species richness is expected to increase with increasing patch size, based on the assumption that the species–area relationship for islands (Preston 1962; MacArthur and Wilson 1967) can be applied to species richness in habitat patches (Holt and others 1995; McIntyre 1995). However, several authors have questioned the usefulness or generality of this assumption (Zimmerman and Bierregaard 1986; Merriam 1988; Wiens 1994), because organisms are much more likely to move among habitat patches than among true islands.

Patch isolation is often predicted to have a negative effect on population density and species richness, because more isolated patches have lower immigration rates, thus reducing the rates of rescue and recolonization (Sjögren Gulve 1994; Dunning and others 1995; Hinsley and others 1995; Kindvall 1995; Enoksson and others 1995). As for patch size, however, patch isolation can have a positive effect on population density for prey or host species that are controlled by enemies, when patch isolation disrupts the enemy's ability to detect the prey (Kareiva 1987; Kruess and Tscharntke 1994; Roland and Taylor 1995). In this case, isolated patches act as refuges for prey/host populations. On the other hand, if most insect predators are generalists, as suggested by Root (1973), then the patch structure that applies to the prey will not normally apply to the predators; isolated patches are not actually isolated for predators that can occur in surrounding habitat. In this case, one would predict a negative effect of patch isolation on prey population density and survival probability.

Increasing disturbance frequency is usually thought to decrease population density and survival probability (Sousa 1984; Grossman and others 1982; Norton and others 1995) and therefore species richness. However, it is also suggested that at very low disturbance frequencies competitive exclusion reduces species richness, leading to a peaked relationship between disturbance and richness, known as the intermediate disturbance hypothesis (Connell 1978; Lavorel and Chesson 1995). Similarly, for patch life span, increasing patch age increases the probability of patch colonization by poorer colonizers, which should lead to an increase in species richness. Increasing patch age also allows population buildup, thus increasing population density and survival probability. However, there may be a peaked relationship between species richness and patch age if very old patches show a decline in species richness, again due to competitive interactions.

The question remains whether any general relationships exist between patch characteristics and population density and/or species richness. The alternative is that effects of patch characteristics on population density and survival are landscape specific and species specific (Lindenmayer and Lacy 1995), requiring detailed studies of each species in each landscape. It is important to determine whether generalizations can be made to allow for the provision of general guidelines in conservation and other management contexts. Our objective was to determine whether general relationships exist between population density and species richness, and patch size, isolation, disturbance frequency, and life span, for insects in an agricultural landscape.

THE STUDY SYSTEM

Human activities impose a spatial and temporal pattern of habitat on a landscape at the human scale, which can accentuate the patchy nature of populations. An obvious example is agricultural activity, which converts a landscape into a patchwork of crop fields of various types, perhaps interspersed with remnant forest, grassland, and/or wetland. For an insect herbivore that specializes on a particular plant type, habitat may be distributed in patches (crop fields) of various sizes, at various distances (degrees of isolation) from each other, with various frequencies of disturbance through farming operations. In addition, patches disappear whenever a field is changed to a different crop type, resulting in a definable patch life span.

Although in general we expect different species to respond at different spatial and temporal scales to a particular landscape (Wiens 1989; Milne 1992), it seems likely that populations of many insects in an agricultural landscape should respond to the scale of the agricultural field in some way. The field represents a discrete habitat area that is internally fairly homogeneous, and large human-caused disturbances such as cutting or pesticide application generally occur at the scale of the whole field. In fact, very few studies of insect populations have been conducted at the whole-field scale. Almost all studies of habitat spatial pattern on insects have been conducted at scales of a few meters [for example, Bach (1980), Kareiva (1987), Bach (1988), Kareiva (1990), and Power (1992); but see Harrison and Thomas (1991)]. Given the large effects of human activities on landscapes, it is important to determine whether there are any general responses of insects to these activities at this scale.

Alfalfa fields in the region surrounding Ottawa, Canada, are disturbed by cutting 1–3 times per growing season. The alfalfa grown in this region is a perennial. Herbicides are not used after the initial planting, and other kinds of plants, such as grasses, invade the alfalfa field over time. About 3–6 years after initial planting, an alfalfa field is usually plowed up and planted in some other crop, such as corn. Likewise, other crops are occasionally plowed up and seeded with a new crop of alfalfa. Therefore, the amount of alfalfa in an agricultural landscape remains approximately constant from year to year, but the locations of the fields shift over the landscape. We studied the relationship between relative density and richness of insects in alfalfa fields and (a) field size, (b) field isolation, (c) field disturbance (cutting) frequency, and (d) field age.

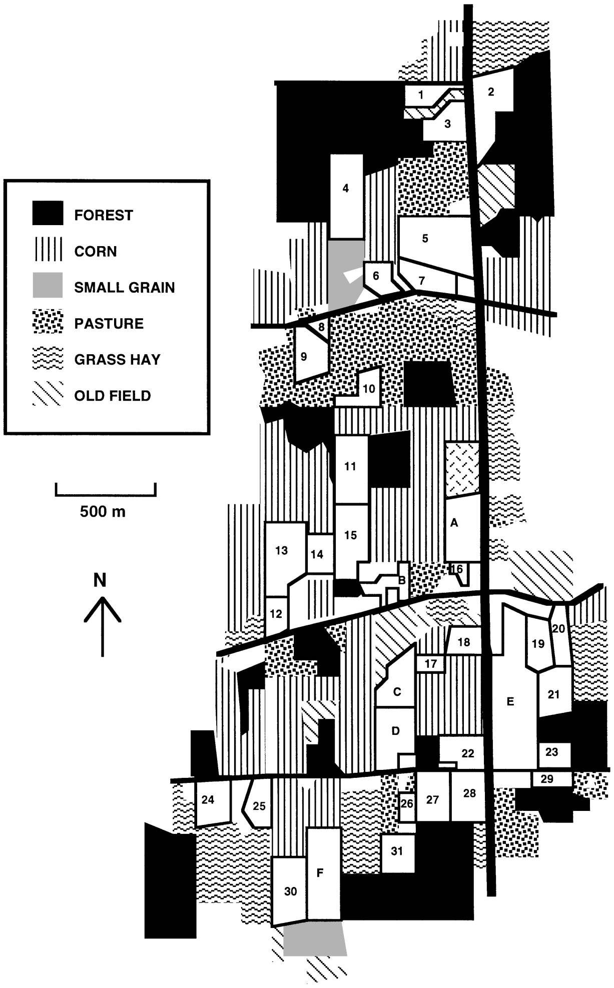

Figure 1. Landscape containing sampled alfalfa fields south of Ottawa, Canada. *Numbers* indicate sampled alfalfa fields. *Letters* indicate alfalfa fields that were not sampled.

METHODS

The study was conducted in an agricultural landscape of approximately 2 × 4 km about 80 km south of Ottawa, Canada (Figure 1). A total of 31 alfalfa fields were sampled for insects weekly from 11 May to 25 August 1993 by sweep-net. The sampler swept such that about half of the net opening was in the vegetation. She walked 40 paces in a transect from north to south in the center of the field, sweeping with each step. All fields were sampled within a single day each week, between 0930 and 1530 h. We varied the order in which fields were sampled during the day, between weeks.

The objective of the statistical analyses was to look for effects of field size, isolation, disturbance, and age on insect relative density and diversity. It was therefore important to correct for local effects of habitat quality on insect relative density and diversity before looking for effects of the patch characteristics, particularly in case the patch characteristics and local habitat quality were correlated. Two likely correlations were between patch age and percent cover alfalfa, and between disturbance frequency (number of cuts) and amount of vegetation. Older alfalfa fields are expected to have a lower percent cover of alfalfa and higher plant diversity because other plants, particularly grasses, gradually invade the fields. Cutting of an alfalfa field removes the canopy, resulting in an increase in percent cover of bare ground. Each week, the vegetation was sampled by randomly placing a 1-m^2 quadrat near the beginning and the end of the sweep-net transect in each field. The percentage cover of alfalfa and other legumes (mainly red clover) and the percentage bare ground within the quadrat were recorded. These values were averaged for each field over the 14-week sampling season to give a single value for each field.

Alfalfa patch sizes (area) and interpatch distances (edge to edge) were measured from aerial photographs. The age of each patch was recorded as 1 (planted the previous season), 2 (planted 2 years before), or 3 (planted 3 or more years before). The number of times each field was cut during the season was also recorded.

All insects in the orders Coleoptera, Collembola, Hemiptera, Homoptera, Lepidoptera, Orthoptera, Psocoptera, and Thysanoptera were identified to family using the method described by Borror and others (1989), and counted. Invertebrate richness at the family level has been shown to correlate highly with richness at the species level (Sepkoski and others 1981).

As just described, the landscape is patchy from the point of view of alfalfa-specialist or legume-specialist insects. However, in addition to such specialists, we expected the samples to contain many generalists that might interact with the landscape as a more homogeneous habitat. We expected the presence of these generalists in the analysis to add noise to relationships at the family level. We therefore selected one family for identification and counting of legume specialists only (there were no major sources of legumes other than alfalfa fields in the landscape). All insects within the family Coleoptera: Curculionidae (weevils) were identified to species. Legume specialists were identified using the methods described by Titus (1911), Arnett (1968), Clark (1971), and A. Howden (personal communication). We use the term *richness* to refer to the number of taxonomic groups, so that family richness is the number of families within each order and weevil species richness is the number of weevil species. All of the insect counts were summed for each field over the 14 weeks of sampling, giving *relative density* values as the number of insects per 560 sweeps (40 sweeps by 14 weeks).

Stepwise multiple regression analyses [RSQUARE option (SAS 1990)] were conducted to examine effects of field size (SIZE), field isolation (distance to next nearest alfalfa field: ISOL), field disturbance rate (number of times the field was cut: CUTS), and field age (AGE) on insect relative density and richness. Both first-order and second-order terms were included for CUTS and AGE, to look for peaked relationships between relative density and richness for these two variables (see the *Introduction*). The square roots of the response variables (relative density and richness) were used in all analyses to satisfy the assumptions of analysis of variance. We conducted the analyses hierarchically in three stages: (a) total relative density and family richness, (b) relative density and family richness of each order, and (c) relative density of each legume-specialist weevil species. By conducting a hierarchical analysis, we were able to determine whether effects at a higher level in the hierarchy were associated with the occurrence of these effects in a subset of the groups in lower levels. For example, an effect of field age on relative density of all insects could represent a common effect across all orders or it could reflect an effect of field age on one (numerous) order.

To control for differences among fields in habitat quality, mean percent cover bare ground and first-order and second-order terms for the mean percent cover legumes from the 1-m^2 quadrant samples were also included in the statistical models. The second-order term was included because of the possibility that insect relative density and richness might be highest when local habitat diversity is high, which may occur at intermediate levels of percent cover legumes. Inclusion of bare ground allowed us to correct for direct effects of cutting (disturbance) on habitat quality. Pesticides were not used on the alfalfa fields; cutting was the only major disturbance.

RESULTS

The total number of insects collected and identified to family was 31,889. Of these, 30,235 were in herbivore-only families. There were 920 weevils, including 6 legume-specialist weevil species. The data are summarized in Table 1.

There was a significant negative correlation between field age and field size ($r = -0.51$). Mean percent cover legumes was negatively correlated with field age ($r = -0.54$) and positively correlated with the number of times a field was cut ($r = 0.40$). There was no significant correlation between total relative density and total family richness. Significant positive correlations were found between relative density and family richness in Lepidoptera, Orthoptera, Psocoptera, and Thysanoptera. There were no significant correlations between different orders (for relative density or family richness). There was one significant correlation between the legume-specialist weevil species densities: *Hypera postica* and *Sitona hispidulus*.

The results of the stepwise regression analyses are presented in Table 2. Recall that habitat-quality variables (percent bare ground, percent legumes, and percent legumes^2) were forced into all models to correct for effects of local habitat quality. All significant ($P < 0.05$) and marginally significant ($0.05 \leq P \leq 0.10$) relationships are shown in Table 2. Significance levels are based on the type III sums of squares, that is, the variation uniquely explained by the given term in the final model. Note that when there is an effect of a squared term (CUTS^2 or AGE^2) but no effect of the corresponding non-squared term, the relationship is monotonic. The

Table 1. Summary Statistics: Sample Size = 31 Fields for All Variables

Variable	Mean	Standard Deviation	Minimum	Maximum
Predictor variables				
% Bare ground	15.96	7.41	2.27	35.48
% Legumes	50.59	17.18	20.10	87.40
Field age: AGE (years)	2.39	0.80	1	3
Field size: SIZE (m^2)	387.68	211.46	80	1017
Field isolation: ISOL (m)	21.77	38.09	1	135
No. harvests: CUTS	1.39	0.72	0	3
All insects				
Total relative insect density	1028.68	401.06	289	1851
Total family richness	24.76	4.04	17	32
Orders				
Relative density				
Collembola	9.39	9.49	0	34
Coleoptera	51.87	27.51	19	126
Hemiptera	264.16	111.91	87	543
Homoptera	680.89	348.64	143	1427
Lepidoptera	2.55	2.06	0	7
Orthoptera	10.35	6.87	1	28
Psocoptera	1.11	1.79	0	8
Thysanoptera	8.35	6.03	0	29
Orders				
Family richness				
Coleoptera	6.84	2.13	3	12
Hemiptera	4.31	1.32	2	8
Homoptera	6.02	0.80	5	8
Lepidoptera	1.95	1.51	0	5
Orthoptera	2.55	1.06	1	4
Psocoptera	0.53	0.62	0	2
Thysanoptera	2.06	0.68	0	3
Weevils				
Hypera postica	3.79	4.71	0	19
Sitona hispidulus	4.84	7.61	0	33
Sitona flavensis	0.81	1.33	0	5
Sitona lineelis	11.35	17.69	0	65
Tichius picirostris	6.40	8.69	0	33
Tichius stephensii	2.44	5.07	0	27

following summary refers only to relationships where $P < 0.05$.

There was no overall effect of field size on insect relative density or family richness. Three orders showed a negative effect of size on either relative density or family richness. One weevil specialist showed a negative effect of field size on relative density.

There was an overall positive effect of field isolation on insect family richness (Figure 2), reflected in the positive effects of isolation on family richness of Hemiptera and Lepidoptera (Table 2).

There was a negative effect of disturbance frequency (CUTS) on overall family richness (Figure 3), reflected in the results for Lepidoptera. Coleoptera relative density was highest at low and high disturbance frequencies and lowest at intermediate disturbance frequency. This was reflected at the single species level for the legume specialist weevils *S. hispidulus* and *T. picirostris* (Table 2).

Total family richness showed a peaked relationship with field age (Figure 4), reflected in the results for Hemiptera. The positive effect of field age on Lepidop-

Table 2. Results of Stepwise Multiple Regressions of Influence of Alfalfa Field Characteristics on Insect Density and Richness

	SIZE	ISOL	CUTS	CUTS^2	AGE	AGE^2	R^2_H	R^2_F
All insects								
ALL DENS							0.165	0.165
ALL FAM		+ (0.022)		− (0.001)	+ (0.014)	− (0.026)	0.222	0.582
Orders								
Collembola density	− (0.001)						0.233	0.495
Coleoptera density			− (0.001)	+ (0.017)	+ (0.035)	− (0.072)	0.210	0.626
Coleoptera richness	− (0.031)						0.127	0.273
Hemiptera density	− (0.043)			− (0.015)	+ (0.070)	− (0.049)	0.060	0.451
Hemiptera richness		+ (0.021)	+ (0.099)	− (0.024)	+ (0.001)	− (0.001)	0.098	0.557
Homoptera density							0.162	0.162
Homoptera richness		+ (0.072)	+ (0.083)	− (0.040)			0.163	0.390
Lepidoptera density		+ (0.018)	− (0.026)			+ (0.001)	0.072	0.519
Lepidoptera richness		+ (0.025)		− (0.042)		+ (0.015)	0.060	0.426
Orthoptera density					+ (0.058)	− (0.097)	0.038	0.236
Orthoptera richness							0.170	0.170
Psocoptera density							0.054	0.054
Psocoptera richness		− (0.064)			+ (0.068)		0.034	0.264
Thysanoptera density							0.070	0.070
Thysanoptera richness							0.113	0.113
Weevils								
Hybera postica							0.515	0.515
Sitona hispidulus			− (0.019)	+ (0.010)			0.285	0.458
Sitona flavensis	− (0.044)			+ (0.083)			0.221	0.407
Sitona lineelis			− (0.003)				0.410	0.582
Tichius picirostris			− (0.074)	+ (0.049)			0.060	0.200
Tichius stephensii			− (0.046)				0.179	0.298

The final models include all terms that were at least marginally significant ($P < 0.1$)*. Presented are the signs of the regression coefficients and, in brackets, the actual probability values based on type III sums of squares, that is, the variation uniquely explained by the given term. Field characteristics are field size (SIZE), field isolation or distance to next nearest alfalfa field (ISOL), disturbance frequency or number of times a field was cut (CUTS), and field age in years (AGE). Local (within-field) habitat quality was included in all models (see* Methods*). Response variables are square root total relative density of insects (ALL DENS), square root total family richness (ALL FAM), square root relative density and family richness of each order (but note there was only one order of Collembola), and square root relative density of each legume-specialist weevil species. The weevil genera were* Hypera, Sitona, *and* Tichius. *Sample size for all models = 31 fields. Relative densities are counts per 560 sweeps. Note that when there is an effect of a squared term (CUTS*^{2} *or AGE*^{2}*) but no effect of the corresponding nonsquared term, the relationship is monotonic.* R^2_H *is the proportion of variation explained by the local habitat quality variables only.* R^2_F *is the proportion of variation explained by the final model, that is, local habitat variables and significant field characteristics variables. Therefore* $R^2_F - R^2_H$ *is the proportion of variation explained by the field characteristics.*

tera family richness reflects the positive effects of field age on Lepidoptera relative density, since relative density and richness are correlated for this order.

DISCUSSION

The observation that species respond in unique ways to landscape pattern [for example, see Fahrig and Paloheimo (1988b) and Capman and others (1990)] has been an impediment to the development of general principles for landscape structure (Arnold 1995; Lindenmayer and Nix 1995). Single-species or two-species studies are the norm in ecological research, largely because elucidation of mechanisms at higher levels of taxonomic aggregation is extremely difficult. However, species-by-species studies cannot tell us whether general responses to landscape structure occur at these higher levels. The aim of this study was therefore to look for general effects of patch characteristics on overall insect density and diversity in an agricultural landscape.

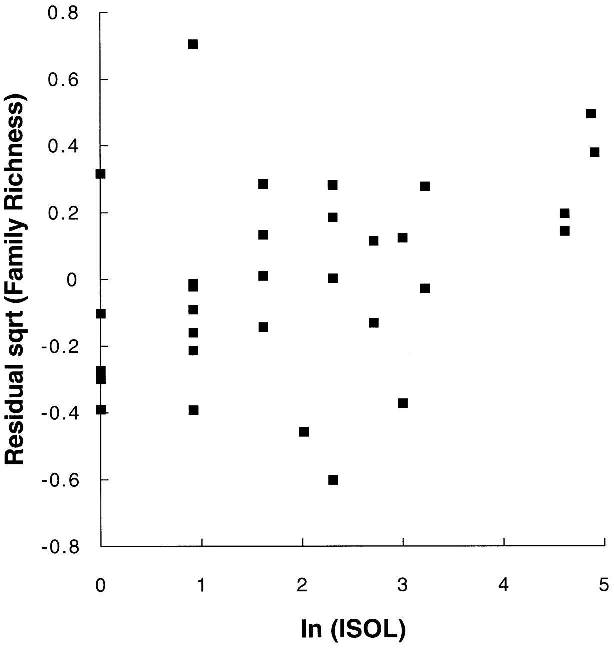

Figure 2. Relationship between total family richness and field isolation (distance in meters to next nearest alfalfa field, ISOL), after accounting for other predictor variables. Points plotted are the residuals from the model: square root total richness = 2.4 − 0.01 (% bare ground) + 0.07 (% legumes) − 0.001 (% legumes^2) − 0.12 (CUTS^2) + 1.4 (AGE) − 0.29 (AGE^2).

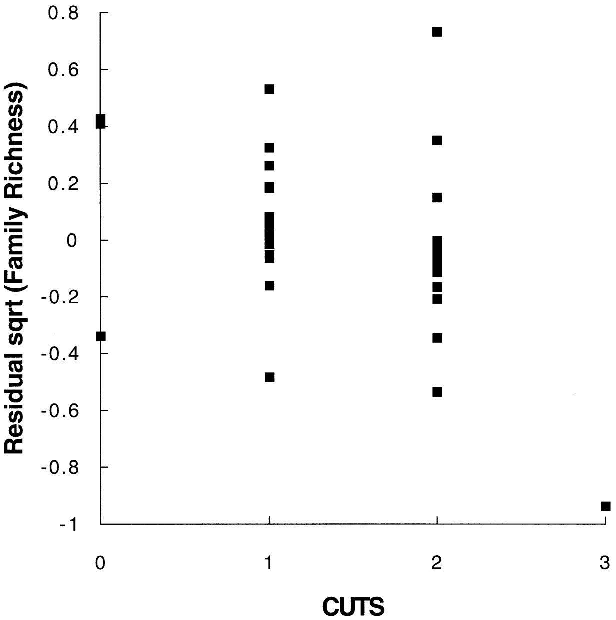

Figure 3. Relationship between total family richness and number of harvests (CUTS), after accounting for all other predictor variables. Points plotted are the residuals from the model: square root total richness = 3.6 − 0.01 (% bare ground) + 0.03 (% legumes) − 0.0003 (% legumes^2) + 0.003 (ISOL) + 0.66 (AGE) − 0.13 (AGE^2).

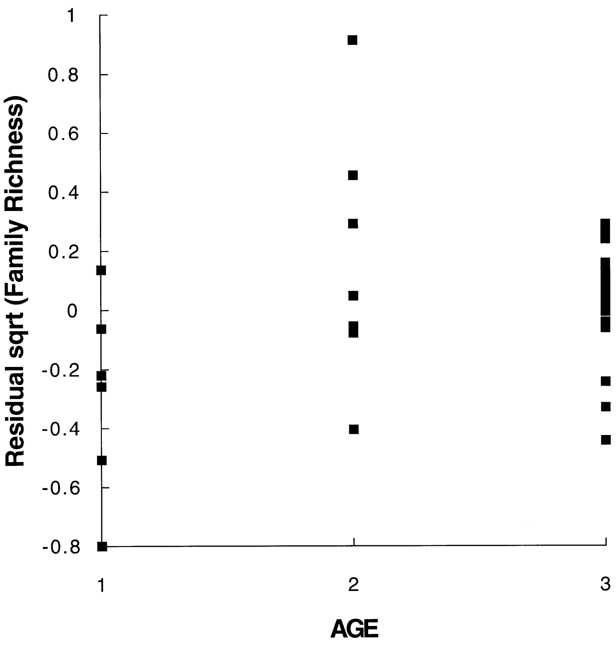

Figure 4. Relationship between total family richness and field age in years (AGE), after accounting for all other predictor variables. Points plotted are the residuals from the model: square root total richness = 4.2 − 0.01 (% bare ground) + 0.05 (% legumes) − 0.001 (% legumes^2) + 0.003 (ISOL) − 0.08 (CUTS^2).

Our study suggests that there are in fact effects of habitat spatial and temporal structure on overall insect richness, despite the idiosyncrasies of species-specific responses to landscape pattern. These effects are (a) more isolated alfalfa fields had higher overall insect richness, (b) fields with higher disturbance frequency had lower overall insect richness, and (c) fields of intermediate age had highest insect richness. In some cases, these patterns were reflected at lower taxonomic levels, but in many cases they were not.

These results are important because they indicate that, although we cannot simultaneously tailor a landscape for each of thousands of species, we may be able to produce desired effects, such as increased biodiversity, at a more general level. For example, the results suggest that we can increase insect diversity in alfalfa fields by cutting the fields only once per season, by using a crop rotation period of about 2 years and by increasing the distance between alfalfa fields, that is, reducing the proportion of the landscape in alfalfa production. The latter would likely imply an increase in habitat diversity at the landscape scale (Jonsen and Fahrig 1997). Of course, these measures may conflict with the goal of maximizing agricultural output. However, the lack of significant patch effects on insect density indicates that insect diversity would increase without an increase in density of insects in the alfalfa fields.

Our results are descriptive, and we could only speculate as to the underlying mechanisms (see the *Introduction*). However, they are unique in that they represent the aggregated response of herbivorous insects to patch characteristics and therefore test the generality of observations based on previous single-species studies. Elucidation of such general patterns is a necessary and important step toward effective ecosystem management.

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