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RESEARCH ARTICLE

Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats

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Abstract The fragmented landscape of the Midwest USA includes prairie remnants embedded in an agricultural matrix, potentially impermeable to dispersing individuals. We examined butterfly responses to local (environmental variables measured within the prairie fragment itself such as vegetative characteristics) and landscape (environmental variables measured up to 2 km surrounding the fragment, but not the fragment itself) factors at 20 prairie remnants in Iowa. Our objectives were to: 1) document how the composition and configuration of the landscape affects butterfly community within the fragment, 2) determine whether explanatory power is gained by including both landscape and local variables rather than only local variables, and 3) analyze differences in butterfly community composition between linear and block shaped fragments. Results from partial least squares regression suggest there are significant effects of the landscape on butterfly community composition at all spatial extents investigated. The local variable that was most highly correlated with butterfly community response was percentage litter, while percentage of roads was the most important variable at all landscape spatial extents. Ordination diagrams clearly separate linear from block sites based on butterfly community composition. Variance partitioning using partial canonical correspondence analysis indicated that landscape variables at all spatial extents add additional explanatory power beyond local variables with little overlap in percentage of variation explained. Our results suggest that butterflies are making decisions based both on the local and landscape environmental factors, thus land surrounding prairie remnants should be included in management decisions.

Keywords Butterflies · Conservation · Floral resources · Habitat fragmentation · Partial least squares regression · Spatial extent · Variance partitioning

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Introduction

Understanding the landscape ecology of fragmented systems is essential to conservation of the flora and fauna in habitat fragments (Fahrig and Merriam 1994). Many landscape scale studies have focused on vertebrates and specifically avian taxa (Mazerolle and Villard 1999), but few have investigated the role of floral resources in the landscape on invertebrates in a highly fragmented landscape. The quality of the matrix surrounding a habitat fragment has impacts on a species' dispersal ability, edge effects, permeability, and isolation (Ricketts 2001; Debinski 2006). In addition, different species or groups of species

perceive the landscape and respond to different landscape features and extents depending on their requirements, sensitivity to disturbance and dispersal abilities (Lord and Norton 1990).

In the Great Plains, the destruction and fragmentation of the tallgrass prairie biome has been particularly severe with over 99% destroyed in most states as a result of conversion to agriculture (Samson and Knopf 1994). Today, all that remains are a few small, protected preserves and numerous smaller, unprotected fragments along railroad right-of-ways and roadsides. Studies indicate that reproduction of butterfly pollinated plant species is often reduced in small populations created by habitat destruction and fragmentation (Hendrix and Kyhl 2000). This evidence leads to the obvious conclusion that butterflies in the Midwest have declined substantially as fragmentation has proceeded.

We are particularly interested in the role tallgrass prairie fragments play in affecting the community composition of butterflies. Prairie fragments often contain high concentrations of floral resources and may be particularly valuable in sustaining butterfly diversity in Iowa where habitat destruction has been so severe. For example, restored roadside prairies in Iowa contain twice as many habitat-sensitive butterflies as do weedy or grassy roadsides (Ries et al. 2001). Fragments can be categorized into two general shapes. Block-shaped fragments are mainly state prairie preserves, which are actively managed with fire. Linear fragments exist along roadsides, railroad rights-of-way, and trails and are generally not actively managed.

From the management perspective, understanding which local and landscape variables affect the butterfly community in fragmented landscapes is critical to sustaining diversity (Saunders et al. 1991). Butterflies forage widely, and studies (Debinski et al. 2001) indicate that local variables such as the distribution and amounts of adjacent landuse types will likely be important in affecting the butterfly community in fragments. The composition and configuration of landuse types (roads, pasture, agricultural fields, etc.) will likely influence the diversity of butterflies at fragments.

Relatively little is known about the factors that control diversity of butterflies in prairie fragments and the relative roles of local and landscape factors. In such a fragmented landscape the distinction between what we refer to as local and landscape variables is relatively clear. Prairie fragments are isolated, have distinct edges and are often surrounded by a monoculture of an agricultural crop. We refer to any environmental variable measured within the prairie fragment itself as a local variable. Local variables including floral abundance (Clausen et al. 2001), width of habitat (Dover 1996; Reeder et al. 2005), shelter (Dover 1996; Dover et al. 1997; Pywell et al. 2004), larval host plant presence (Pywell et al. 2004), habitat quality (Schneider and Fry 2001; Collinge et al. 2003; Jeanneret et al. 2003), and adjacent land use (Sparks and Parish 1995) have been shown to affect butterflies at the extent of the habitat patch itself. We refer to any environmental variable measured in the landscape surrounding the fragment, but not the fragment itself as a landscape variables. Landscape variables at larger spatial extents such as connectivity (Haddad 1999b; Haddad and Baum 1999; Sutcliffe et al. 2003), size of habitat patches in the landscape (Dennis and Shreeve 1997; Steffan-Dewenter and Tscharntke 2000; Tscharntke et al. 2002; Krauss et al. 2003), isolation (Clausen et al. 2001; Sawchik et al. 2003), edge permeability (Haddad 1999a; Ries and Debinski 2001; Schultz and Crone 2001; Merckx et al. 2003), and landscape heterogeneity (Debinski et al. 2001; Ricketts 2001; Schneider and Fry 2001; Sutcliffe et al. 2003) have also been shown to influence butterflies.

The spatial extent at which butterflies actually forage is a logical place to begin analyses of landscape resource abundance and diversity on butterfly community composition. Butterfly dispersal is not random (Conradt et al. 2000; Dover and Fry 2001; Kindlmann et al. 2004; Cant et al. 2005) but rather based on local and landscape variables. Butterflies routinely make dispersal bouts at distances of 1 to 2 km (Harrison 1989; Wahlberg et al. 2002; Schneider 2003; Auckland et al. 2004) and daily movements of 200 to 600 m (Jones et al. 1980; Auckland et al. 2004); therefore we used landscape spatial extents of 0.5 to 2.0 km in our study.

Different groups of butterflies may be responding to different environmental variables and spatial extents. Mutually exclusive butterfly habitat groups were classified a priori based on host plant and nectar resources (Opler and Krizek 1984; Ries et al. 2001; Shepherd and Debinski 2005; Reeder et al. 2005;

Table 1 Latin and common names for each species including acronyms

Latin name	Common name	Acronym	Habitat	Abundance	
			Group[a]	Linear	Block
Anatrytone logan	Delaware Skipper	ALOGA	HS	20	2
Ancyloxypha numitor	Least Skipper	ANUMI	DT	2	3
Atalopedes campestris	Sachem Skipper	ACAMP	DT	0	1
Celastrina neglecta	Summer Azure	CNEGL	DT	5	0
Cercyonis pegala	Common Wood Nymph	CPEGA	HS	82	53
Colias eurytheme	Orange Sulfur	CEURY	DT	95	37
Colias philodice	Clouded Sulfur	CPHIL	DT	7	2
Cupido comyntas	Eastern-Tailed Blue	CCOMY	DT	185	72
Danaus plexippus	Monarch	DPLEX	DT	34	67
Euphyes dion	Dion Skipper	EDION	HS	0	1
Eurema lisa	Little Yellow	ELISA	DT	2	0
Lycaena dione	Gray Copper	LDION	HS	1	0
Oarisma poweshiek	Poweshiek Skipper	OPOWE	HS	4	0
Papilio polyxenes	Black Swallowtail	PPOLY	DT	5	9
Pholisora catullus	Common Sootywing	PCATU	DT	7	0
Phyciodes tharos	Pearl Crescent	PTHAR	DT	35	19
Pieris rapae	Cabbage White	PRAPA	DT	10	3
Polites mystic	Long Dash Skipper	PMYST	HS	62	5
Polites peckius	Peck's Skipper	PPECK	DT	12	6
Polites themistocles	Tawny-Edged Skipper	PTHEM	DT	5	1
Pyrgus communis	Checkered Skipper	PCOMM	DT	2	0
Satyrium titus	Coral Hairstreak	STITU	HS	2	0
Satyrodes eurydice	Eyed Brown	SEURY	HS	0	3
Speyeria cybele	Great Spangled Fritillary	SCYBE	HS	18	2
Speyeria idalia	Regal Fritillary	SIDAL	HS	8	99
Vanessa atalanta	Red Admiral	VATAL	DT	13	4
Vanessa cardui	Painted Lady	VCARD	DT	19	33

[a] HS represents butterflies classified as habitat-sensitive whereas DT represents disturbance-tolerant butterflies

Group distinctions are listed for each species as well as total abundance at block and linear sites summed across years

Table 1). Disturbance-tolerant (DT) species survive well in agricultural and/or urban areas and occur throughout Iowa. Habitat-sensitive (HS) species are associated with native prairie and require prairie dependent plants for either larval or adult resources.

Objectives

Our first objective was to determine how much explanatory power is gained by including landscape variables in our analyses as compared to using only local variables. We expected the addition of landscape variables to the local model would increase our ability to explain the variability in butterfly community composition between sampling sites. Our second objective was to document how the landscape composition and configuration at multiple spatial extents affects the butterfly community composition at prairie fragments. We anticipated that landscape floral resources would be positively related to community composition. In addition, we wanted to determine whether or not we gain more information by collecting data on landscape floral resources as compared to readily accessible data on landuse types. Our final objective was to determine whether there are differences in community composition of butterflies

between linear and block sites. We wanted to determine if there are differences in the local and landscape variables between linear and block sites and if so, how the butterfly community is responding to the differences.

Methods

Sampling sites

Sampling sites refers to prairie fragments (block or linear) where butterflies were sampled. In 2003, we sampled the butterfly communities at seven block and ten linear sites. In 2004, we sampled the same 17 sites as 2003, and added three block sites to increase our sample size to 20. All sites were remnant tallgrass prairies located in the northwest quarter of Iowa, far enough from each other so that the 2 km buffers did not overlap between two nearby sites. The sample size of block sites was constrained by our a priori qualifiers for accepting a site to sample such as a minimum size of 40,000 m^2 and a minimal proportion (<30%) of non-native, aggressive plant species at the site. The specific block sites sampled represent a range of sizes (100,000–650,000 m^2) and the landscape surrounding them varied considerably in the relative amount of landuse types. At each block and linear site, we established two 100 m by 5 m transects marked with survey flags. Transect lengths were typical of those used in previous pollinator studies (Ries et al. 2001; Reeder et al. 2005). Transect locations were randomly selected from among areas not dominated by wetland vegetation and at least 50 m from each other.

Butterfly sampling

In 2003 and 2004, we surveyed each site once for adult butterflies three times during the growing season (June, July, and August). Butterfly surveys were conducted between 0930 h and 1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/h and the sun was shining. Butterfly surveys were conducted by walking each 100 m transect at a pace of 10 m/min and observing butterflies within 2.5 m on either side and in front of the observer (Thomas 1983). During each visit, all butterflies (including skippers) were counted and identified on the wing if possible; otherwise they were netted. The amount of time used to handle individuals, record field notes, etc., was not counted towards sampling effort.

Quantification of local and landscape resources

Floral resources at the local extent were estimated by a direct count of flowering ramets in each 100 m transect during all rounds of butterfly sampling. We choose to survey the floral resources rather than host plants because of the direct comparison between adult butterflies and nectar sources. Relative proportions of forbs, native grass, non-native grass, litter, and bare ground were estimated for each transect. Approximations of vegetation variables were averaged using values from two observers to avoid observer bias.

In order to identify the spatial extent at which butterflies respond to landscape features, we chose to use spatially nested circular buffers (i.e., larger extents include smaller extents; Fig. 1) rather than separate annular rings (i.e., concentric rings, independent ellipses or circles at all extents). The literature is divided as to the preferred approach with examples of both annular rings (Pearson 1993; Graham and Blake 2001) and nested buffers (Bergin et al. 2000; Ribic and Sample 2001). Because spatially nested buffers are not statistically or biological independent, we did not include multiple extents in a given model but rather compared the correlation between butterfly assemblage and each spatial extent.

We quantified resources in the landscape surrounding each site within a 2 km radius centered in the middle of the site. We analyzed landscape data using nested spatial extents of 0.5, 1.0, 1.5 and 2.0 km because different butterflies may respond to landscape features at different spatial extents. We used digital color infrared orthophotographs with a resolution of 1 m pixels taken in 2002 along with ArcMap 8.3 (Environmental Systems Research Institute 2004) to divide each 2 km radius landscape into visually distinct, homogeneous polygons based on differences in landuse types. Grain size was a minimum of 6 m by 50 m for two reasons: 1) butterflies are known to have a perception ability of 50 m to a suitable patch (Harrison 1989) and 2) to include linear features in the landscape such as

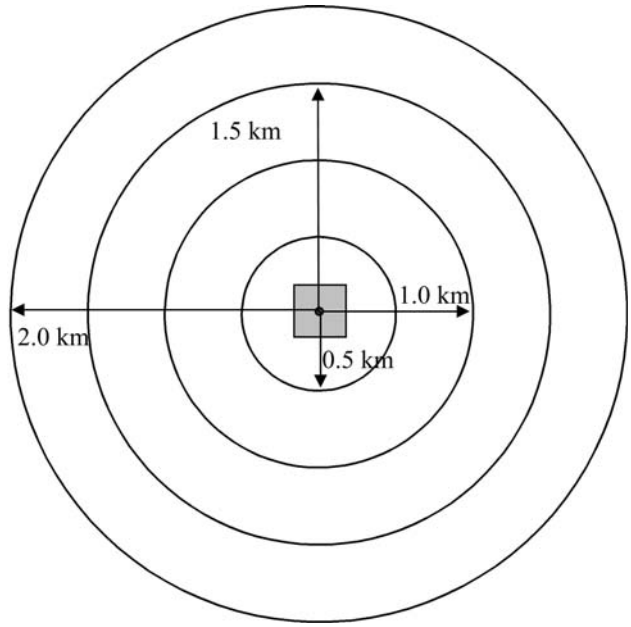

Fig. 1 Schematic drawing of spatially nested landscape extents. The center rectangle represents the sampling site with the center of the site marked with a dot. Buffers at 0.5 km increments radiate out from the center of the sampling site

roadsides (Ries et al. 2001) and buffer strips (Reeder et al. 2005) known to influence butterflies. Grain size was constant across extents. The boundaries of the polygons for half of the sites were checked in 2003 and the remaining half in 2004. We used visual inspection by walking, observing from the road with binoculars and driving along polygon boundaries to assess any recent landuse changes and to assign a floral resource index (FRI) value of high or low to each polygon on the basis of the richness and abundance of all forb species in the polygon (see Hines and Hendrix 2005 for a complete description of FRI). Our ''high'' FRI value corresponds to the Hines and Hendrix rating of a value of three and above (2005), where ''low'' includes below a FRI of three. The landscape dataset was created in conjunction with another project including other pollinator taxa and therefore includes all forb species rather than only those forbs known to be associated with butterflies.

Data analysis

From the initial set of biologically meaningful variables, where pairs of independent variables were highly correlated ($r > 0.7$), the variable that was most strongly correlated with other variables was eliminated from analyses. Our local variables included: litter coverage (LITTER), floral abundance (FABUND) and site size (SIZE; Table 2). Our landscape variables included: distance to nearest polygon with high floral resource density and diversity (MINDIST), percentage coverage non-linear grassland (GRASS), percentage coverage road (ROAD), and percentage coverage of polygons with high floral resource density and diversity (FRI; Table 2). We chose to use metrics that included high floral resources because this may be a large enough magnitude to attract butterflies to a polygon in the landscape, although there is little data to support this (but see Kuussaari et al. 1996; Luoto et al. 2001). Landscape variables at all extents did not include the area encompassed by the sampling site. Arcsin square-root transformations were applied to percentage variables and log transformations were applied when abundance and environmental data were not normally distributed. Local variables and butterfly response variables were averaged over the two years of sampling.

For a community-based analysis, we used partial least squares (PLS) regression to investigate the correlation between the species abundance matrix and environmental variables at different spatial extents (ter Braak and Verdonschot 1995). We chose this method over other ordination techniques because PLS relaxes restrictions on colliniarity among groups

Table 2 Local and landscape variables and associated descriptions

Scale/variable	Unit	Description	Biological significance
Local			
LITTER	%	Percent cover of litter	Overwintering habitat for larvae Kopper et al. (2000)
FABUND	count	Floral abundance	Food resource for adults e.g., Steffan-Dewenter and Tscharntke (1997)
SIZE	m^2	Site size	Habitat availability e.g., Krauss et al. (2003)
Landscape			
GRASS	%	Proportion of each buffer that is non-linear grassland	Habitat availability composition; e.g. Schneider and Fry (2001)
ROAD	%	Proportion of each buffer that is road	Measure of connectivity/fragmentation composition; e.g. Haddad (1999a)
FRI	%	Proportion of each buffer with high floral resource density	High forb diversity composition; e.g. Dennis et al. (2003)
MINDIST	m	Distance to nearest polygon with high floral resource density within each buffer	Habitat availability configuration; e.g. Dennis et al. (2003)

Each landscape variable was measured at four spatial extents (0.5, 1.0, 1.5 and 2.0 km) from the center of each site, but metrics do not include the site itself

of variables and is more biologically meaningful than using factor analysis separately on the species and environmental matrices (Johansson and Nilsson 2002). PLS explains the maximum covariation between species abundance and environmental variables at each extent. Before performing PLS we standardized all abundance and environmental variables to a mean of zero and variance of one. We performed PLS using all species with total abundance greater than 10, disturbance-tolerant, and habitat-sensitive species. PLS was performed with the simples.fit procedure of the pls library (version 1.2–1) in R (Mevik 2006), which uses the SIMPLS algorithm described by de Jong (1993).

We used the correlation of the first X (environmental matrix) to the first Y (species abundance matrix) component at each extent (local, 0.5, 1.0, 1.5, and 2.0 km) from the PLS results to find the extent at which there is the greatest correlation. To determine the level of significance between the correlations at all extents, we performed a permutation test. The permutation procedure involved randomly shuffling rows of the Y matrix (i.e., maintaining site species abundances but randomizing sites) and performing the PLS regression for 10,000 iterations (the observed PLS was the first iteration). To discern if the observed correlations differed significantly, we calculated all pairwise contrasts between correlation coefficients and determined the empirical probability (P_{rand}) of finding an equal or greater difference using random distributions generated from the permutation procedure.

We also investigated the variable importance projection (VIP) values for each landscape variable at each extent (Johansson and Nilsson 2002). VIP-values quantify the influence of each variable on the ability to explain the variation in the response variables. VIP-values greater than one are considered the most relevant, although this does not indicate the direction of influence (i.e., positive or negative). We used model equations from PLS to examine the ability of environmental variables to explain species abundance. Model equations were created using local variables, landscape variables, and the global model which included all variables from both local and landscape extents.

We used the ordination diagrams created using PLS to analyze differences in butterfly community composition between linear and block sites. General patterns of differences in local and landscape variables between linear and block sites were analyzed using multivariate analysis of variance (MANOVA).

We used partial canonical correspondence analysis (pCCA) in R-project (R Development Core Team 2004) to show the percent of the variation in butterfly community composition that is explained by local

variables alone, landscape variables alone, and the overlap of local and landscape variables for each landscape extent (0.5–2.0 km; Borcard et al. 1992). The percent of the variation explained is the ratio of the sum of the constrained eigenvalues to the sum of the unconstrained eigenvalues (total inertia). We first conducted a canonical correspondence analysis (CCA) using local variables. For each landscape extent we then conducted a series of constrained ordinations: one using the local variables as covariables, one using the landscape variables as covariables and one on landscape variables alone to partition the variance.

Results

We identified 27 species of butterflies and 1,057 individuals. We eliminated woodland species (*Papilio glaucus* and *Enodia anthedon*) from all analyses to focus our results on grassland butterflies.

Local versus landscape

The correlation of the first component of the species matrix to the first component of each environmental matrix from the PLS regression was plotted at all extents (local, 0.5–2.0 km; Fig. 2). All correlations were significant ($P < 0.003$). There were no significant differences between any of the pairwise comparisons of extents ($P_{rand} > 0.226$). For a species level approach we compared the ability to explain species abundance between local and 0.5 km extent variables

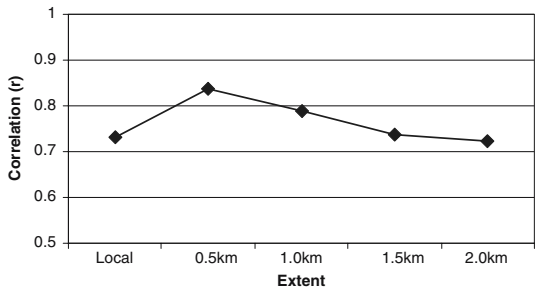

Fig. 2 Coefficients are plotted for the correlation between the first PLS component of the species matrix with the first PLS component of the environmental matrix at all extents. All correlations are significant ($P < 0.001$), although none of the pairwise comparisons of extents are significantly different from each other

by sorting the list of species and groups by R^2 for each extent (Table 3). The results were the same for all landscape extents, but we compared the local with the 0.5 km extents here for simplicity. We are able to explain abundance of *Phyciodes tharos* relatively well using local variables ($R^2 = 0.30$–0.46), but lack explanatory power with landscape variables. Disturbance-tolerant species, *Danaus plexippus*, and *Speyeria idalia* abundance can be explained relatively well at local and landscape extents. *Speyeria cybele* and *Anatrytone logan* abundance can be explained using landscape variables, but not local variables. Habitat-sensitive species abundance cannot be explained using either local or landscape variables.

We compared the ability to explain the variation in butterfly abundance at the local versus the landscape scale using pCCA. Landscape variables alone explained between 19.8% and 23.4% of the variation, depending on extent, and local variables alone explained 25.3% of the variation in community composition (Fig. 3). The amount of overlap in the proportion of the variance explained by the local and landscape variables ranged between 0.8% and 5.5%, depending on landscape extent, with decreasing shared percentage as landscape extent increased. The overall percentage explained by local and landscape variables ranged from 42% to 46%.

Linear versus block

Landscape variables were not constant in magnitude across spatial extents and differed between linear and block sites (Table 4). Percentage road and high landscape floral resources did not show a consistent pattern across extents whereas minimum distance to nearest patch of high floral resources increased with extent. Percentage of the landscape that is grassland decreased with extent for block sites but increased with extent for linear sites. The MANOVA of local variables showed no significant differences between linear and block sites ($df = 1$, Wilk's $\lambda = 0.86$, $P = 0.26$). MANOVAs of landscape variables showed significant differences between linear and block sites ($df = 1$; Wilk's $\lambda = 0.29, 0.37, 0.47, 0.48$; $P < 0.001$, 0.003, 0.016, 0.019) at all spatial extents: 0.5, 1.0, 1.5 and 2.0 km respectively.

Ordination diagrams derived from PLS allow us to visualize the influence of the environmental variables

Table 3 Local and 0.5 km landscape regression coefficients associated with explanatory equations

Species	Local models				Landscape models					Global model
	LITTER	SIZE	FABUND	R^2	FRI	ROAD	MINDIST	GRASS	R^2	R^2
Danaus plexippus	−0.01	0.30	0.49	0.35	0.50	−0.40	−0.19	−0.37	0.39	0.72
Speyeria idalia	0.24	0.56	−0.32	0.45	0.04	−0.32	0.47	−0.20	0.37	0.69
Anatrytone logan	0.36	−0.24	0.06	0.22	−0.19	0.58	−0.34	0.17	0.46	0.57
Speyeria cybele	–	–	–	NS	0.70	0.26	0.00	−0.16	0.54	0.57
Disturbance-tolerant	−0.23	−0.45	0.44	0.46	0.16	0.20	0.11	−0.31	0.22	0.56
Pieris rapae	0.23	−0.33	0.23	0.20	−0.25	0.44	−0.06	0.02	0.26	0.49
Phyciodes tharos	−0.39	−0.41	0.26	0.39	–	–	–	–	NS	0.47
Cercyonis pegala	0.43	0.19	−0.06	0.21	–	–	–	–	NS	0.42
Polites peckius	0.40	−0.13	0.52	0.28	–	–	–	–	NS	0.41
Habitat-sensitive	0.27	0.09	−0.33	0.25	–	–	–	–	NS	0.30
Polites mystic	0.14	−0.29	−0.23	0.22	–	–	–	–	NS	0.27

Response variables included abundance of each species found in more than 20% of all sites and total abundance for each of two groups (habitat-sensitive and disturbance-tolerant). *R*-square corresponds to the ability to explain abundance given local variables, landscape variables or global model. Species with $P > 0.05$ were omitted and non-significant (NS) model details are removed for simplicity

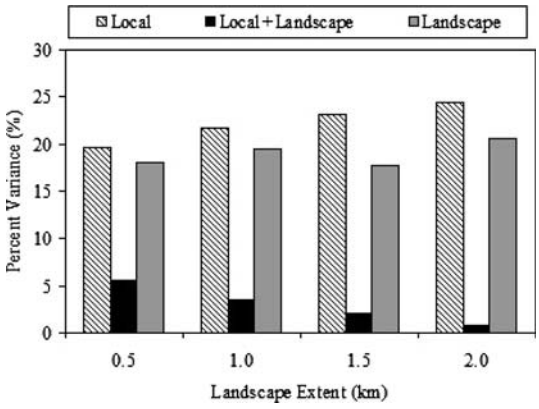

Fig. 3 Percentage of the variance in the species abundance matrix which is explained by each extent of environmental variables measured from the pCCA. Percent variation explained by local variables alone was 25.3%. Percent variation explained by landscape variables alone was 23.4, 22.9, 19.8 and 21.2% at landscape extents of 0.5, 1.0, 1.5 and 2.0 km respectively. Percent variation explained by local plus landscape variables was 5.5, 3.5, 2.0 and 0.8% at landscape extents of 0.5, 1.0, 1.5 and 2.0 km respectively

on sites, species and site shape. Given the biplot where the local variables were plotted along with the species and site scores we can infer that site size is strongly correlated with block sites (Fig. 4a) because the SIZE arrow points in the direction of block sites. Proportion of litter is associated with linear sites (Fig. 4a). Patch floral abundance is not associated with one habitat shape over the other. *D. plexippus*, *Papilio polyxenes*, *S. idalia* and *Vanessa cardui* were associated with block sites. *A. logan*, *Colias eurytheme, Polites mystic*, *Polites peckius* and *S. cybele* were associated with linear sites. *Oarisma powesheik*, a state threatened species, was found only at linear sites.

We also created a biplot with landscape variables at the 0.5 km extent (Fig. 4b). Ordination diagrams of the 1.0–2.0 km extents resembled the 0.5 km biplot but were omitted here for simplicity. Percentage of the landscape that is roads was most associated with linear sites while percentage grassland and the minimum distance to the nearest high floral resources patch were most associated with block sites. *S. idalia* and *Ancyloxypha numitor* were associated with block sites. *A. logan*, *C. eurytheme, Celastrina neglecta*, *Pholisora catullus*, *P. mystic*, and *Pieris rapae* were associated with linear sites.

Butterfly responses

VIP-values for local variables indicated that percent litter and patch floral abundance are the most relevant variables to explain variation in the butterfly community composition. VIP-values for each landscape variable were plotted against all landscape

Table 4 Summary statistics for all local and landscape variables for linear and block sites

Variable	Block		Linear	
	Mean	Min–Max	Mean	Min–Max
Local variables				
LITTER (%)	11.25	2.50–25.00	15.75	7.50–26.25
SIZE (m^2)	339,864	114,322–665,870	29,346	7899–76740
FABUND (count)	2,640.50	139–6,210	2,178.50	828–3,485
Landscape variables				
FRI:0.5 km (%)	0.00	0–0	0.00	0–0
FRI:1.0 km (%)	1.33	0–9.82	0.10	0–0.60
FRI:1.5 km (%)	1.27	0–6.98	0.09	0–0.56
FRI:2.0 km (%)	1.02	0–3.82	0.28	0–2.05
ROAD:0.5 km (%)	1.21	0–2.95	2.65	0.99–5.23
ROAD:1.0 km (%)	1.44	0.46–2.96	1.60	0.81–3.30
ROAD:1.5 km (%)	1.28	0.69–2.23	1.37	0.80–2.36
ROAD:2.0 km (%)	1.28	0.74–1.68	1.44	0.97–2.17
MINDIST:0.5 km (m)	203	0–445	73	0–285
MINDIST:1.0 km (m)	262	0–587	173	0–997
MINDIST:1.5 km (m)	525	43–1,326	173	0–997
MINDIST:2.0 km (m)	525	43–1,326	357	0–1,841
GRASS:0.5 km (%)	26.86	0–62.66	2.45	0–6.76
GRASS:1.0 km (%)	19.97	0–59.07	4.86	0–14.05
GRASS:1.5 km (%)	15.80	0.36–53.68	5.17	0.76–11.04
GRASS:2.0 km (%)	14.19	0.33–48.54	6.14	0.62–17.24

Local variable statistics are averaged over rounds and years

extents (Fig. 5). Percentage of the landscape that is roads is an influential variable at all extents. The minimum distance to the nearest high floral resources patch is marginally influential at all extents. Percentage of the landscape that is grassland becomes more important with increasing extent. Percentage of the landscape that is high floral resources is marginally influential at 0.5 km and has decreasing influence with increasing extent.

Model equations from PLS were evaluated by examining the R^2 from plotting observed versus predicted abundance for each species (Table 3). The majority of the species responded to percent litter (10 out of 13, 77%) and floral resource abundance (9 out of 13, 69%) positively and site size (8 out of 13, 62%) negatively. Individual species showed mixed responses to all landscape variables. Percent of the landscape that contains high floral resources (6 out of 10, 60%), roads (6 out of 10, 60%), grassland (6 out of 10, 60%), and minimum distance to the nearest high floral resources patch (5 out of 10, 50%) were positively associated with butterfly abundance. Again, we only report landscape variables at the 0.5 km extent for simplicity.

Discussion

Local versus landscape

Our results show that butterfly community composition is significantly correlated with all extents, although there is not one extent that is any more correlated than any other. The proportion of coverage that is road at all landscape extents influences butterfly community composition in prairie fragments.

Butterfly composition was more correlated with floral resources than with grassland in the landscape

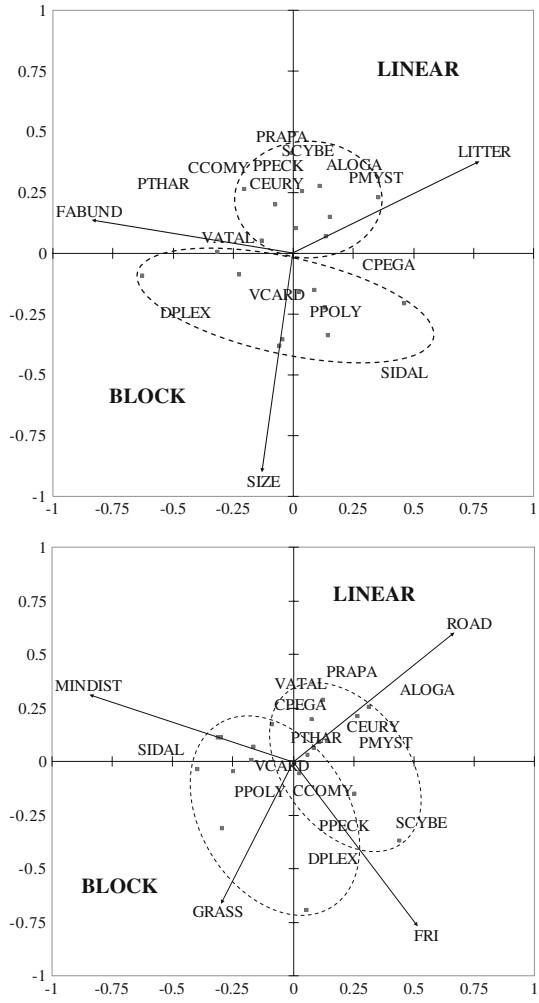

Fig. 4 Partial least squares ordination biplot based on a species by site matrix of abundant butterflies (abundance >10) where site scores, species scores and environmental variables are plotted in two dimensions at the (**a**) local and (**b**) 0.5 km landscape extents. Dotted ellipses represent groupings of sites by shape. Butterfly species scores are denoted by abbreviations of Latin names (Table 1). The *X* and *Y* axes are the first and second components respectively

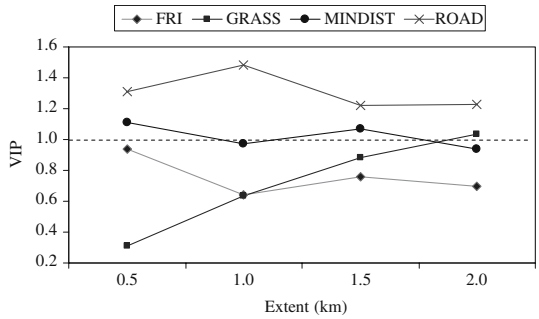

Fig. 5 Variable importance projection (VIP) values from PLS regression are plotted against all landscape extents. Values greater than one are considered high importance. Proportion of road is an important variable at all landscape extents. Proportion of the landscape that is grassland is important at larger extents of 1.5 and 2.0 km

at small landscape extents. Although grassland becomes more important with increasing extent, this result may be an artifact of increasing variance of the metric with extent. Explanatory models for individual species confirm that floral resources in the landscape are an important indicator for which the majority of species responded positively to and to a stronger degree than the amount of grassland in the landscape (Table 3). Based upon these results, if a land manager is interested in sustaining butterfly communities, creating a grassland conservation buffer that includes a high diversity of forbs will provide the greatest success.

Understanding landscape configuration and composition added considerable ability to explain variation in community composition beyond what the local variables explained. Landscape metrics alone added additional explanation of the variation in butterfly community composition beyond what the local variables explained. The percent variation explained by local variables was comparable to that of landscape variables at all extents. Variance partitioning has been used in other multi-scale studies and some have found similar results with taxa other than butterflies with respect to the amount of overlap (Titeux et al. 2004), and the total percentage of variation explained by local and landscape variables (Chust et al. 2003; Williams and Wiser 2004). Others have found opposite results with high overlap between local and landscape factors (Chust et al. 2003; Miller et al. 2004; Williams and Wiser 2004) and with local factors explaining more variance than landscape factors (Miller et al. 2004; Titeux et al. 2004). In a review of all studies that compared local versus landscape effects, Mazerolle and Villard (1999) found that in general, landscape variables explain a small percentage of the variance as compared to the local environment. Contrary to these general trends, our results suggest that in the Midwestern prairie ecosystem, landscape variables explain a relatively large percentage of the variance in butterfly community composition.

We know that butterflies are capable of moving within the landscape to high-quality patches, which suggests they are either assessing patches from a distance or moving within the landscape and sampling (Matter and Roland 2002). Our results support the hypothesis that butterflies are making decisions based both on the local and landscape environmental factors. Additionally, our results suggest that the sphere of landscape influence for butterflies in Midwest prairies occurs at all extents investigated. This is consistent with other studies (Jeanneret et al. 2003; Krauss et al. 2003) that examined extents of 200 and 250 m respectively. Other multi-scale studies found scales of 5 km to be the landscape scale most correlated with butterfly diversity (Bergman et al. 2004). Our results differed from our expectation of a decrease in the correlation values with increasing landscape extent, indicating that perhaps we did not include a large enough extent in our analyses.

Linear versus block habitat

The PLS ordination diagrams (Fig. 4) clearly separate linear from block sites based on butterfly community composition. Local biotic variables were not significantly different between linear and block sites, indicating that although the butterfly community differed, this difference was probably not a result of difference in local biotic variables, but rather a difference in site size or shape. The landscapes surrounding linear sites had less grassland and fewer polygons with high floral diversity in closer proximity to the site than block sites, whereas linear sites had more roads in the immediate landscape. Thus, the habitats are very different between linear and block sites and species are responding to these differences.

Butterfly responses

Species responses to local and landscape variables differ remarkably as did the amount of variation explained at both extents. Habitat-sensitive species as a whole were marginally positively correlated with litter (especially *A. logan*, *Cercyonis pegala*, and *S. idalia*) whereas disturbance-tolerant species were negatively correlated with litter, with some exceptions (*P. peckius*). Habitat-sensitive species such as *A. logan* and *P. mystic* were highly correlated with linear sites, suggesting these species may be responding to the increased amount of litter at linear sites. Generally, in order to increase habitat-sensitive butterfly abundance, a manager would want to increase or maintain the amount of litter through a decrease in fire frequency and intensity. Increased litter may be ecologically important because it provides increased moisture and cover for overwintering larvae (Kopper et al. 2000).

Disturbance-tolerant species were negatively correlated with site size. Disturbance-tolerant species may be responding positively to linear habitats because of the larger edge to area ratio and thus increased disturbance. This result however, may be an effect of site size on species composition because the linear sites are significantly smaller in size than block sites.

Individual species responses to landscape variables varied and this variation can be explained by analyzing life histories of each species. Roads are highly and positively correlated with some species such as *A. logan*, *C. neglecta*, and *P. catullus* which all use weedy plant species (Poaceae, *Melilotus officinalis* and *Chenopodium album* respectively) commonly found in roadside ditches as hostplants. *A. logan* may be responding positively to roads because of the associated increased connectivity grassy roadsides provide. *S. idalia*, a species of special concern in Iowa, is positively correlated with the minimum distance to nearest polygon with high floral resources. In order to increase the abundance of *S. idalia*, patches of habitat should be created with high floral diversity in close proximity to prairie fragments.

Limitations

Similar to previous studies (Luoto et al. 2001), there are some limitations in our ability to explain butterfly assemblages at any extent. The amount of variation explained is relatively low, suggesting that there are additional variables that are influencing community composition. We have no data on host plant cover in the sites, and this variable may influence habitat-sensitive species because of their specificity for certain larval hostplants.

One solution to understanding the ways in which adult butterflies use linear and block habitats would

be to study differences in behavior (Ouin et al. 2004). This method is still one step away from truly studying the reproductive biology of butterflies and how the local and landscape environment affects source-sink dynamics in linear versus block habitats.

In order to interpret fully the mechanisms behind the correlations of each spatial extent to butterfly abundance patterns, we need to collect data on movement (Mazerolle and Villard 1999). Behavioral data on movement is essential to understanding movement and dispersal at an extent larger than a patch (Lima and Zollner 1996). There are two studies, both of one species of butterfly which documented detection ability of 70 m to unfamiliar habitat and 125 m to familiar habitat (Conradt et al. 2000) and 50 m to a suitable patch (Harrison 1989). A tracking study reports a perceptual range of 100–200 m for five species of butterflies (Cant et al. 2005). The reason for the lack of data on dispersal and movement is the difficultly associated with tracking individual butterflies. Modeling may be a good alternative to field studies given the constraints of mark recapture studies. Sutcliffe et al. (2003) modeled movement of two common butterflies in a fragmented landscape and found that increasing the amount of linear features in landscapes improved movement by increasing connectivity between suitable habitat patches.

Conservation implications

Responses to different local and landscape variables differ drastically across species. Assuming that the goal of management is to preserve biodiversity with a focus on conserving species sensitive to disturbance, managers should consider the ability of roadsides to provide connectivity. Dispersal rates are lower in highly fragmented landscapes, indicating that connectivity and spatial configuration need to be taken into account (Baguette et al. 2003). Given our findings, we argue that preservation and restoration of prairie fragments on railroad rights-of-way is essential to sustaining butterfly diversity in the tallgrass prairie ecosystem of the Midwestern US, including conservation of state threatened species such as *O. powesheik*, which was only surveyed at linear sites and may be barely hanging on in isolated fragments.

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A cross-taxonomic comparison of insect responses to grassland management and land-use legacies

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Abstract. Many species of plants and animals associated with grasslands are rare or declining due to habitat loss and degradation. Although grassland plants and insects evolved in the context of both grazing and fire, the appropriate use of grazing and fire has been debated among those concerned with protecting insect communities. We established an experiment to test insect responses to three grassland management treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle), (2) graze-and-burn (burning of entire tract with free access by cattle), and (3) burn-only. Because we expected that land-use legacies could also affect insect abundance and diversity, we evaluated effects of time since fire, grazing history, remnant history (remnant or reconstructed grassland) and pre-treatment vegetation characteristics, which were assumed to be a legacy of prior land-use. Butterflies (Lepidoptera), ants (Hymenoptera: Formicidae), and leaf beetles (Coleoptera: Chrysomelidae) were surveyed for three years to compare their responses to each of these treatments as measured by abundance, richness and species diversity. Each of these taxa is relatively diverse and was expected to have the potential to have strong negative responses to grazing and burning, but we predicted more positive responses to patch-burn grazing. Our results showed that land-use legacies affected insect abundance, richness and diversity, but treatments did not. Ant abundance was lower in tracts with a history of heavy grazing. Ant species richness was positively associated with pre-treatment time since fire and vegetation height and negatively associated with pre-treatment proportion native plant cover. Butterfly abundance was positively associated with pre-treatment litter cover. Leaf beetle diversity was positively associated with pre-treatment native plant cover, and leaf beetle abundance was negatively associated with time since fire. Our results indicate that land-use legacies can exert more influence on grassland insect community composition than current management, but the particular aspects of these land-use legacies that are important vary across insect taxa. The implications of these finding are that (1) land-use legacies should garner more attention in grassland management and (2) conservation of grassland insect communities will be improved by taxon-specific analysis of land-use legacy variables.

Key words: burning; butterflies; Chrysomelidae; Formicidae; grassland; grazing; insect diversity; Iowa; land-use legacy; Lepidoptera; Missouri; tallgrass prairie.

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Introduction

Managing and restoring grassland ecosystems for insect communities has been a topic of heated debate for the past few decades, and this is particularly true in the tallgrass prairie ecoregion of the U.S. The use of fire is contested among those concerned with protecting insect communities (Swengel 1998, Panzer and Schwartz 2000, Cook and Holt 2006), and concerns have been raised as to the compatibility of burning smaller grassland tracts relative to the conservation of insect populations within these tracts (Panzer 2002). Burning can greatly influence the presence-absence of arthropod species on a particular grassland tract, and species differ in their tolerances for fire (Warren et al. 1987, Swengel 1996). In addition, the time since fire can influence the species present (Reed 1997). Many insect species decline immediately after a burn (Swengel 2001) while other species increase (Gibson et al. 1993, Larsen and Work 2003, Moranz 2010), and the trajectory of abundance relative to time since burn can vary among species even within the same taxonomic group (Vogel et al. 2010).

Grazing, like fire, can affect the species abundance and diversity of grassland fauna (Andresen et al. 1990, Sutter and Ritchison 2005, Warui et al. 2005) and flora (Towne et al. 2005), and controversies have ensued regarding the potential impacts on insects. Grazing sometimes reduces grassland insect diversity (e.g., Stoner and Joern 2004), even in areas where it has little effect on the plant community (Milchunas et al. 1998), yet in other locations increases insect species richness and Shannon diversity (Joern 2005). The intensity of grazing can influence the direction of the insect response. For example, insect species richness was greater in grasslands with low-intensity grazing than those with high-intensity grazing (Kruess and Tscharntke 2002). Ants have been less extensively studied in grasslands, but in Argentine subtropical forest, ant community composition varied along a gradient of grazing intensity (Bestelmeyer and Wiens 1996). Ant species were distributed based on their preference for litter versus bare ground; both of these variables were affected by grazing, but can also be altered by burning.

Patch-burn grazing is a management approach that combines both fire and grazing and has potential for insect conservation because it creates heterogeneity in both the spatial and temporal patterns of grazing and burning (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Whereas uniform application of either grazing or fire can simplify the landscape, different levels of grazing creates habitat heterogeneity which can support a more diverse set of invertebrate species (Tscharntke and Greiler 1995, Swengel 2001). Patch-burn grazing involves subdividing a pasture into sections which are burned sequentially over multiple years. Large ungulates focus their grazing on the recently burned patches (Coppedge and Shaw 1998, Vermeire et al. 2004), creating a mosaic of (1) heavily grazed/recently burned patches, (2) patches that were burned six to 18 months earlier and are dominated by forbs after the ungulates have moved on to more recently burned patches, and (3) patches dominated by grass and senesced vegetation. Engle et al. (2008) found that the increased habitat heterogeneity generated by patch-burn grazing was reflected in increased heterogeneity of insect biomass compared to pastures under traditional homogeneity management.

However, in addition to current management, many grasslands are influenced by legacies of prior land-use (Burke et al. 1989, Trimble 1999). Plowing, grazing, and fire can leave immediate effects as well as enduring consequences on ecosystem structure and function for centuries after the processes have been operative (Foster et al. 2003). Land-use legacies can be measured via abiotic properties of the ecosystem (e.g., soil carbon, nitrogen content, soil compaction), as well as biotic components (e.g., current plant or animal community composition). It is often difficult to determine the history of land use, but this history can be important when evaluating grassland restoration success.

To better understand the responses of invertebrate communities to fire and/or grazing, a variety of investigators have quantified invertebrate community responses before and after disturbances (Nekola 2002, Larsen and Work 2003, Engle et al. 2008, Doxon et al. 2011). Due to taxonomic challenges, these responses are often quantified at the order or family level. Although these assessments provide important information, the interpretation of the results can be challenging because of the diversity of life history traits within a family (which may include herbivores, predators, or decomposers and species with life stages that include belowground as well as aboveground activity). Alternatively, much of the research that has been done at the species level to assess responses has focused on a single family or order.

Here we describe the results of an experimental grassland management project that compared abundance, species richness, and diversity responses of ants (Order Hymenoptera, Family Formicidae), butterflies (Order Lepidoptera), and leaf beetles (Order Coleoptera, Family Chrysomelidae) to three grassland treatments: burn-only, graze-and-burn, and patch-burn graze. These taxa are relatively diverse in grassland ecosystems and were expected to respond strongly to grazing, burning, or the combination thereof. Trager (1998) argues that the sheer biomass of ants compared with other insect families justifies research concerning ants. Additionally, ants often serve as ecosystem engineers by altering habitat through burrowing and foraging (Jones et al. 1994, Wagner et al. 2004) and have been shown to respond to anthropogenic change across a wide range of habitats (e.g., Majer and Nichols 1998, Bestelmeyer and Wiens 2001). Butterflies are excellent subjects for ecological management studies because they are relatively easy to identify in the field and can be highly responsive to disturbance via direct as well as indirect effects (Waltz and Covington 2004, Nelson 2007). Chrysomelid (leaf) beetles have been less extensively examined in grassland ecosystems, but are a diverse group of herbivores, and, like butterflies, many species have specialized associations with host plants (Clark et al. 2004, Barney and Hall 2011).

All three of these insect taxa could be expected to have strong responses to burning, grazing, and vegetative composition and structure due to their dependence on vegetation for food and habitat as well as the importance of bare ground or litter for nesting and overwintering habitat. In addition, there is value in cross-taxonomic comparison of these responses to determine whether a broader group of insects is responding similarly to disturbance patterns and/or habitat characteristics. With that in mind, we tested for effects of treatment (burn-only, graze-and-burn, and patch-burn graze) on abundance, richness, and diversity of each taxon, while simultaneously testing for effects of pre-treatment covariates, including land-use history variables (grazing history, remnant history [i.e. remnant versus reconstructed grassland]), fire history, and pre-treatment vegetation variables (i.e., composition and structure). The vegetation present at the beginning of our study is in fact the legacy of prior land use (McGranahan 2008, McGranahan 2011) and was expected to affect insect community richness and diversity patterns. We made the following predictions:

1. Patch-burn grazed tracts will have higher species richness and diversity compared to tracts managed using more traditional techniques (i.e., graze-and-burn and burn-only tracts) due to non-burned refugia, spatial heterogeneity of grazing pressure, and increased structural heterogeneity of the vegetation.
2. Prior land use (plowing, heavy grazing by cattle, and burning) will have left legacies that affect abundance, richness, and diversity of each of the three taxa (ants, leaf beetles and butterflies). Specifically, tracts that were plowed and later reconstructed, and tracts with a history of heavy grazing will have lower richness and diversity than grassland remnants and those that lacked a history of heavy grazing. Tracts with longer pre-treatment time since fire will have higher diversity and abundance of all three insect taxa.
3. Variation in pre-treatment vegetation characteristics (e.g., proportion native plant cover) that are legacies of land-use history will affect abundance and diversity of each of the three insect taxa, but these patterns may vary across the taxonomic groups

based upon habitat preferences for nest sites (ants), overwintering sites (butterflies), and species-specific plant use (all three taxa).

Methods

Study tracts

In 2006, we selected 12 tracts for a controlled experiment to test the effects of fire and grazing treatments on vegetation structure, plant community composition, and terrestrial insect community composition in the Grand River Grasslands of southern Iowa and northern Missouri, USA (Appendix A). The tracts, which ranged in size from 15 to 34 ha, occurred within a mixture of private and public grasslands. They were allocated to one of three treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle, $N = 4$), (2) graze-and-burn (burning of entire tract with free access by cattle, $N = 4$), and (3) burn-only (burning of entire tract with no grazing, $N = 4$). From 2007 through 2009, tracts receiving the first two treatments were stocked with cattle at about 3.4 animal unit months per ha between May 1 and October 1. Each tract was divided into three patches of approximate equal area. In patch-burn graze tracts, natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries to the extent possible. Each year, a different patch within each patch-burn graze tract was burned in early spring (mid-March). Tracts in the burn-only and graze-and-burn treatments were burned in their entirety in spring 2009, except for one burn-only tract, which was burned in spring 2008. Thus, the fire-return interval was the same across all three treatments.

Land-use history was classified in terms of remnant history as well as fire and grazing history. Remnants were defined as grassland tracts that had never been plowed, whereas reconstructed grasslands were planted from seed in bare soil. Pre-treatment time since fire denoted the number of years since fire had been applied to each tract as of 2006 (values ranged from 0 to 15 years). Grazing history was classified as either having a history of severe grazing or not. Although some of the tracts had long histories of severe grazing, we defined our pre-treatment legacies in terms of the previous three years (2003–2005) for consistency in this analysis. The land-use history of each tract was determined by interviewing landowners and governmental land managers who owned/managed the tracts.

Vegetation sampling

Pre-treatment vegetation variables were used as covariates to enable us to separate treatment from legacy effects. Pre-treatment vegetation data were collected in 2006 at the transect-level to describe plant community composition, and at the patch-level to describe plant composition and structure. Plant community composition was sampled twice during the summer season and measured at the species level in two permanently-marked Whittaker plots (Stohlgren et al. 1995) per patch (i.e., $N = 6$ Whittaker plots per tract) as described in McGranahan (2011). The canopy cover value for each species was the maximum canopy cover value observed. From Whittaker plot data, we calculated the proportion of native plant canopy cover in each patch, using the following equation: proportion native plant cover = total native plant canopy cover/(total native plant canopy cover + total exotic plant canopy cover).

During July of 2006 we measured pre-treatment plant functional group composition and vegetation structure in thirty 0.5-m^2 quadrats that were placed systematically within each patch as described in Pillsbury et al. (2011). Variables measured included Robel vegetation height (Robel et al. 1970), percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum* (Schreb.) S.J. Darbyshire (tall fescue). Cover measurements used the following cover classes: 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100% (Daubenmire 1959). Center points of each cover class were averaged within each patch ($N = 30$ quadrats/patch) and tract ($N = 90$ quadrats/tract).

Sweep net sampling

Sweep net surveys of terrestrial invertebrates were conducted in each tract twice per year during the periods of major emergence (June to early July and mid-July to early August) from 2007–2009. Surveys were conducted along 50-m transects parallel to the eastern edge of each

Whittaker plot with a starting point 10 m east of the north-center coordinate of each plot, resulting in 12 samples per tract per year (2 transects per patch × 3 patches per tract × 2 sampling periods per year). Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds. Surveys were conducted by a single individual walking south along each transect at a constant pace, holding a net with both hands with the net handle directed forward and the net opening pointed sideways. The net was swept at a constant pace from side to side 40 times, where one sweep includes the complete back and forth swing in both directions, as the individual traveled the transect. Completing 40 sweeps was preferred to traveling exactly 50 m to maintain constant effort. Insects were carefully transferred from the net to a plastic zip lock bag at the completion of each transect and frozen until they could be sorted. Due to the greater than expected labor costs of identifying insects, only samples from each patch's northern transect were identified, resulting in six identified samples per tract per year. Samples from each patch's southern transect remain frozen for future processing if funding permits.

Sweep net samples were sorted to family level, preserved in ethanol in vials categorized by tract, replicate, and date, and stored until they could be later identified to species. L. Winkler, with the assistance of J. Trager, identified ant species. R. Barney identified the chrysomelid leaf beetles.

Butterfly sampling

Butterflies were sampled via Pollard walk transects (Pollard and Yates 1993) twice per year from 2007–2009. Sampling was spaced temporally to cover the major emergence periods (June to early July and mid-July to early August). One 100 × 5-m transect was established parallel to the west side of each Whittaker vegetation sampling plot, with a starting point 10 m west of the north-center coordinate of the plot, resulting in 12 samples per tract per year (2 transects per patch × 3 patches per tract × 2 sampling periods per year). During butterfly sampling, an observer walked the transect at a steady pace (~10 m/min) and recorded data on butterflies seen within the 5 m × 5 m area in front of the observer (extending 2.5 m to each side of the transect, and 5 m forward). Each butterfly was identified to the species level. Specimens that could not be identified in the field were captured and identified in our lab. Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds.

Data analysis

Insect count data from the June and July sampling periods were added together, so that a single value of each response variable was obtained for each transect each year. For each of three major taxa, we calculated four response variables: abundance, species richness, Shannon diversity, and Simpson diversity. Abundance was defined here as the total number of individuals of each taxonomic group (butterflies, ants, or leaf beetles) found per transect. Species richness was calculated as the number of unique species found per transect. Shannon diversity was calculated as $H = -\sum(p_i \ln(p_i))$ and Simpson diversity was calculated as $D = 1 - \sum p_i 2$, where p_i is the percentage of ith species and ln is the natural log. Shannon diversity is a measure of species evenness, while Simpson diversity is a measure of species dominance (Magurran 2004). Due to the difference in total samples available, for butterflies, response variables were calculated for two transects per patch per year, whereas for ants and leaf beetles, response variables were calculated for one transect per patch per year.

Univariate data analysis.—We performed mixed model analysis of covariance using the statistical software package SAS version 9.2 (SAS Institute 2008) to test for effects of treatment and year on response variables for our three focal taxa after accounting for the influence of pre-treatment covariates. We viewed plots of residuals versus fitted values. If residuals failed to exhibit an approximately normal distribution, analyses were re-run with transformed response variables. Values of pre-treatment covariates were obtained in 2006. Before performing analysis of covariance, we reviewed the grassland insect literature to select a list of potential variables to serve as covariates. Then, we tested for correlations among those vegetation variables; when correlation coefficients were 0.70 or greater, the variable more likely to be associated with insect density (based

on our literature review) was retained as a covariate whereas the other was excluded to reduce multicollinearity. Pre-treatment covariates entered in all analyses of covariance included: grazing history, remnant history, time since fire, proportion of native plant cover, forb cover, Robel vegetation height, litter cover, and the cover of bare ground. Backward elimination was performed to remove insignificant covariates from each analysis of covariance, with $\alpha = 0.05$ used as criterion for retaining each covariate. When analysis of covariance indicated a significant effect of treatment, or a significant treatment by year interaction, we used differences of least squares means as our multiple comparison procedure.

Multivariate data analysis.—We used nonmetric multidimensional scaling (NMDS) to describe separately the structure of the ant, butterfly, and leaf beetle communities. NMDS is an unconstrained, distance-based ordination technique in which the distance between samples in ordination space corresponds to the similarity in community structure among samples. Ordinations were performed using VEGAN (Oksanen 2009), a package of community analysis functions for the statistical software R (R Development Core Team 2010). In order to avoid spurious results, species occurring in only one transect were not included in the ordinations. Bray-Curtis distance was used as the measure of dissimilarity among grassland transects.

For all ordinations, transect-level abundance data from 2007–2009 were plotted together, i.e., each point on the ordination represents community composition of a transect in a particular year. Thus, the vectors that describe the insect responses to vegetation variables represent the composite response across all three years. Subsequently, we tested for correlations between ordination axis scores and values of 11 pre-treatment vegetation variables derived from the same Whittaker plot locations: proportion of native plant cover, plant species richness, Robel vegetation height, percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum*. Vegetation variables significantly correlated with one or more ordination axes at $\alpha \leq 0.05$ were plotted as vectors.

Results

Over three years, the numbers of species and total individuals collected were as follows: ants: 14 species and 5101 individuals; butterflies: 33 species and 2048 individuals; leaf beetles: 44 species and 1189 individuals. Fig. 1 presents tract-level patterns of abundance (Fig. 1A), richness (Fig. 1B), Shannon diversity (Fig. 1C), and Simpson diversity (Fig. 1D) for each treatment, whereas Fig. 2 represents tract-level patterns of abundance and richness relative to grazing history and remnant history (with graphs of diversity indices omitted for simplicity's sake). However, the statistical results we wish to emphasize are those of Table 1 because the ANCOVA results evaluate responses of transect-level abundance, richness, and diversity after accounting for the influence of covariates, which is a more accurate representation of the responses. Grassland management treatments had no main effects on any of the four response variables (abundance, species richness, Shannon diversity and Simpson diversity) measured for each taxon, and had interactive effects (with year) only on butterfly abundance (Table 1). Because treatment showed no significant main effects, we present ordinations of each of the communities superimposed with vectors defining significant pre-treatment vegetation variables relative to species distributions but without designation of treatment type. Year affected response variables for each of the three taxa. Regarding significant year effects, we refer the reader to Table 1 and save further mention of this for the discussion.

Ants

Grasslands with a recent history (2003–2005) of grazing had fewer ants ($F = 7.75$, df = 1, 10, $P = 0.019$), than grasslands without such a history (Table 1, Fig. 2A). No other factors, including remnant history (Fig. 2C) affected ant abundance (Table 1). Ant species richness was influenced by three pre-treatment covariates (Table 1, Fig. 2B, D): remnant history (with remnants having greater species richness than reconstructed grasslands), proportion native cover (negative correlation), and Robel vegetation height (positive correlation). Remnant grasslands had greater Shannon diversity of ants than reconstructed

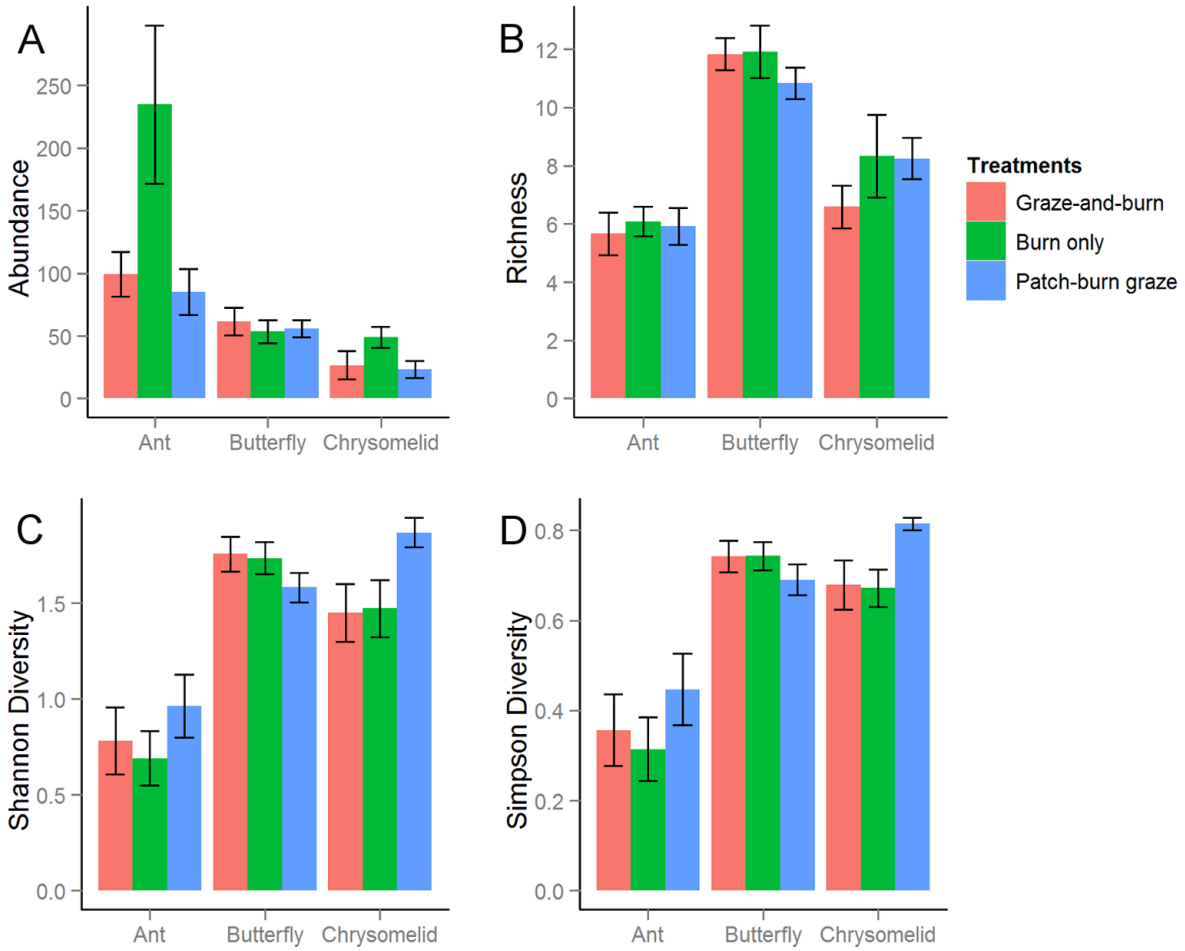

Fig. 1. Treatments compared for (A) abundance, (B) species richness, (C) Shannon diversity, and (D) Simpson diversity of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

grasslands ($P = 0.002$, Table 1). Three pre-treatment covariates were positively correlated with Shannon diversity: cover of bare ground, Robel vegetation height, and time since fire (Table 1). Several findings on Simpson diversity were consistent with those obtained on Shannon diversity: (1) ant diversity did not differ among treatments, (2) remnants had greater ant diversity than reconstructions ($P < 0.001$), and (3) Robel vegetation height was positively correlated with ant diversity ($P < 0.001$). However, two unique results were obtained using Simpson diversity. Tracts having a recent history of heavy grazing had lower ant diversity than tracts without that history ($P = 0.027$), and proportion of native cover was negatively correlated with ant diversity ($P = 0.002$).

Ordination of ant data (Fig. 3) showed that grasslands dominated by *Formica montana,* the most abundant ant species in our study (representing 81% of all ants captured), separated from grasslands with several less dominant species (*Camponotus americanus*, *Formica subsericea*, *F. exsectoides* and *Lasius alienus*). The ant community ordination was correlated with one vegetation variable: pre-treatment Robel vegetation height ($r^2 = 0.06$, $P = 0.025$).

Butterflies

Treatment and year interacted to affect butterfly abundance ($P = 0.029$) (Table 1): both grazing treatments exhibited high interannual variation

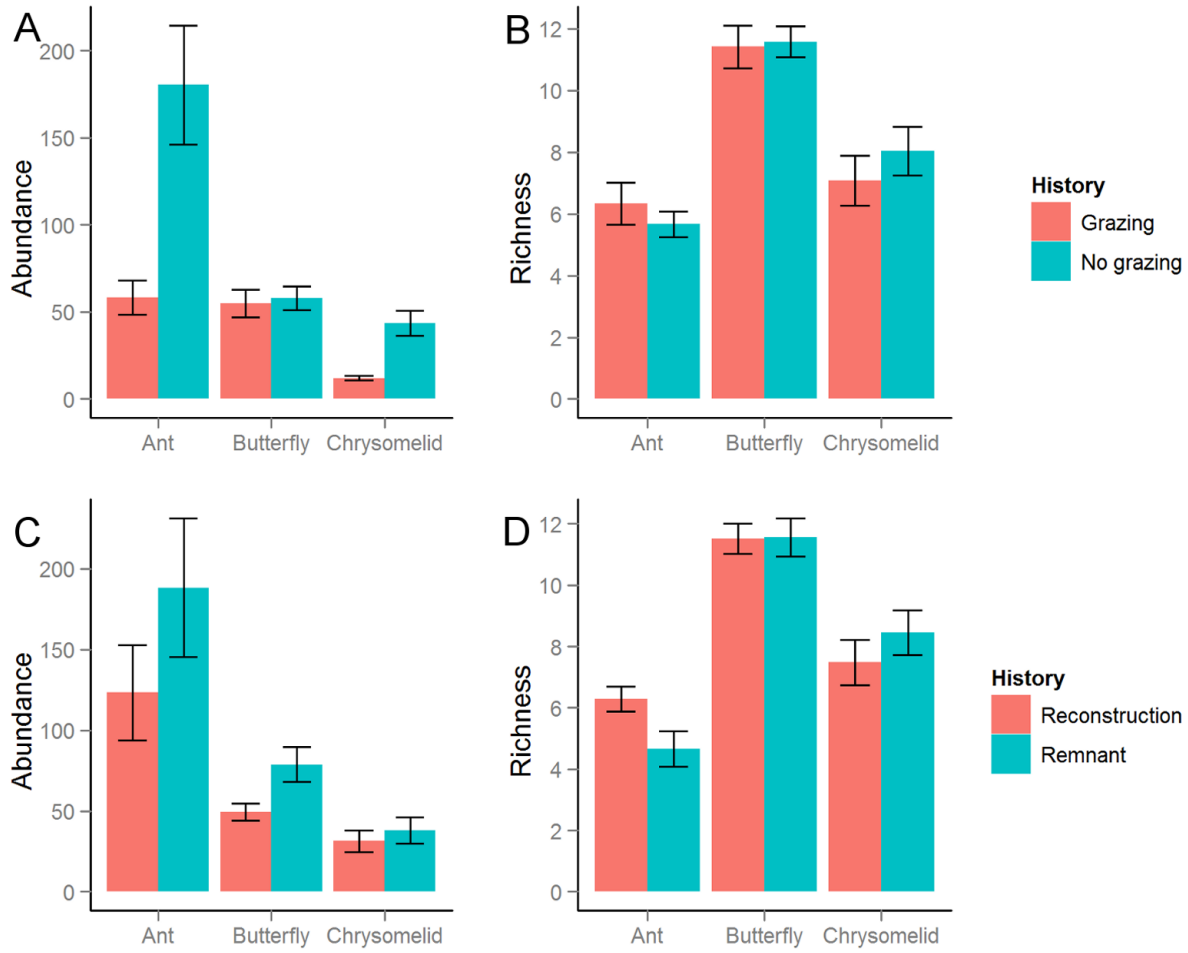

Fig. 2. Effects of grazing history on (A) abundance and (B) species richness, and effects of remnant history on (C) abundance and (D) species richness of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

in butterfly abundance ($P < 0.001$ for each treatment), whereas abundance did not vary among years in the burn-only treatment. Pre-treatment litter cover was positively associated with butterfly abundance ($P = 0.011$, Table 1). No pre-treatment covariates were associated with butterfly species richness, or with either diversity index (Shannon or Simpson) (Table 1, Fig. 2A–D). Ordination of butterfly community structure (Fig. 4) showed that three habitat specialists (*Cercyonis pegala*, *Lycaena hyllus* and *Speyeria idalia*) and one habitat generalist (*Danaus plexippus*) were associated with grasslands having greater pre-treatment proportion native cover ($r^2 = 0.41$, $P = 0.002$), forb cover ($r^2 = 0.20$, $P = 0.008$), and woody cover ($r^2 = 0.07$, $P = 0.012$). Species at the opposite end of the primary ordination axis included two exotic, habitat-generalist species (*Thymelicus lineola* and *Pieris rapae*) and three native, habitat-generalist species (*Cupido comyntas*, *Colias philodice*, and *Papilio polyxenes*) that were associated with pre-treatment values of cool season grass cover ($r^2 = 0.07$, $P = 0.06$) (Fig. 4).

Leaf beetles

Pre-treatment values of time since fire were negatively associated with leaf beetle abundance ($P = 0.01$) (Table 1). Pre-treatment values of proportion native cover were positively associated with leaf beetle species richness ($P = 0.018$) and Shannon diversity ($P = 0.022$), whereas no covariates were significant predictors of Simpson

Table 1. Associations between independent variables and insect response variables.

	Ants				Butterflies				Leaf beetles			
Independent variables	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM
Experimental variables												
Treatment												
Year			**	***	***	**			**	*	**	*
Treatment × Year					*							
Legacy variables												
Grazing history	−*			−*								
Remnant history		+*	+**	+***								
Time since fire			+*						-**			
Proportion native cover		−*		−**						+*	+*	
Forb cover												
Bare ground cover			+**									
Litter cover					+*							
Robel vegetation height		+***	+***	+***								

Notes: Legacy variables are covariate data from 2006. Response variables are based on data from 2007, 2008 and 2009, and are abbreviated as follows: AB = abundance, RIC = species richness, SHA = Shannon diversity, SIM = Simpson diversity. Blank cell indicates that independent variable was not a significant predictor of response variable. Asterisks indicate that independent variable was a significant predictor of response variable: * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$. Plus and minus signs indicate whether the relationship between variables was positive or negative. For the independent variable "grazing history" a minus sign indicates that grasslands with a recent history of grazing had lower values of response variable than grasslands without a recent history of grazing. For the independent variable "remnant history" a plus sign indicates that remnant grasslands had higher values of response variable than grassland reconstructions.

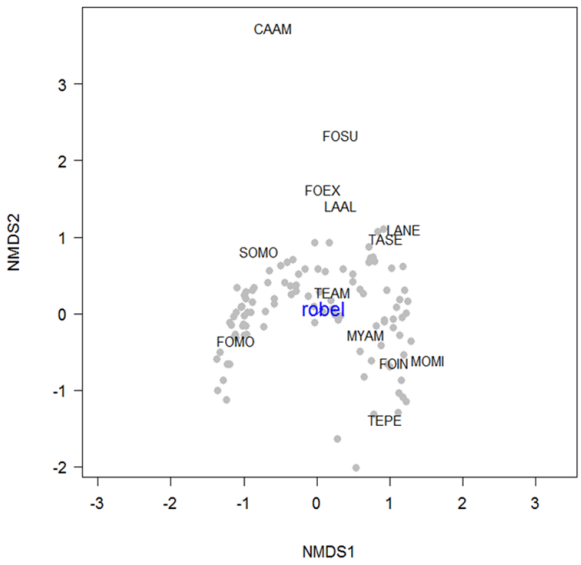

Fig. 3. Ant community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet, see Appendix B). Pre-treatment Robel vegetation height (robel) is significantly correlated with the ordination and is plotted as a vector to demonstrate its relationship to ant community composition.

diversity. Leaf beetle community structure (Fig. 5) was correlated with pre-treatment variables including proportion native plant cover ($r^2 = 0.50$, $P = 0.013$), warm season grass cover ($r^2 = 0.40$, $P = 0.024$), cool season grass cover ($r^2 = 0.26$, $P = 0.038$), and legume cover ($r^2 = 0.17$, $P = 0.025$). Some of the more common species of leaf beetles (e.g., *Zygogramma suturalis*, *Epitrix* spp., *Paria thoracica*, *Diabrotica barberi* and *D. undecimpunctata*) were widely separated in ordination space.

Discussion

The results of this research show that land-use legacies had far more influence on insect distribution and abundance patterns than currently imposed management treatments, even after three years of treatment implementation. Our prediction that patch-burn grazed tracts would have higher species richness and diversity of ants, butterflies, and leaf beetles than tracts managed for homogeneity was not supported by our results. In fact, this experiment showed few effects of burning and grazing treatments on invertebrate abundance, richness and diversity measures. These results contrast strongly with responses observed for grassland birds within the same tracts (Pillsbury et al. 2011).

We propose two hypotheses to explain this

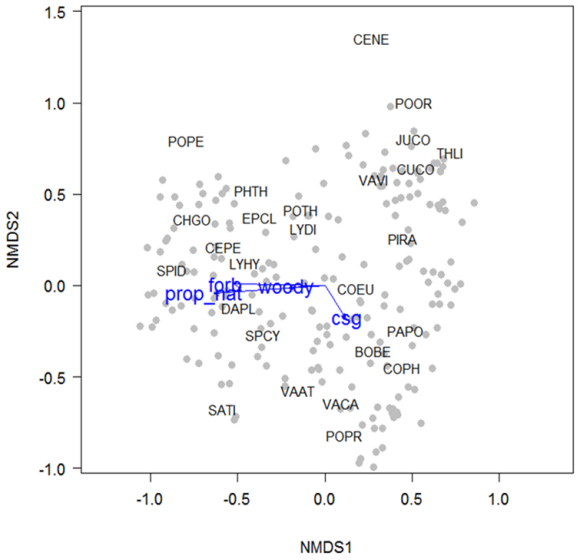

Fig. 4. Butterfly community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix C). Four pre-treatment vegetation variables significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with butterfly community composition: cool season grass cover (csg) woody plant cover (woody), forb cover (forb), and proportion of native plant cover (prop_nat).

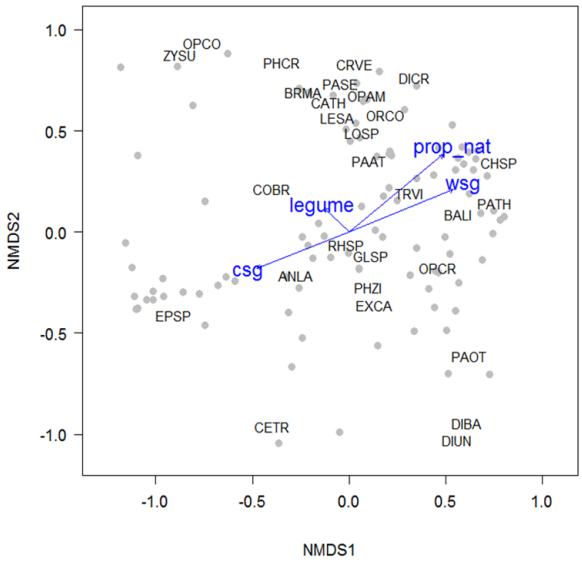

Fig. 5. Chrysomelid community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix D). Four pre-treatment vegetation variables that are significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with chrysomelid community composition. These variables are cool season grass cover (csg), legume cover (legume), proportion of native plant cover (prop_nat) and warm season grass cover (wsg).

unexpected outcome. First, for some taxa, particularly ants, legacies of previous land-use appear to have had significant impacts on determining local distribution and abundance. These legacies may have diminished our ability to observe treatment effects, and three years of these treatments are not enough to alter differences in abundance, diversity and composition that were established by heavy grazing. This might be especially so for ants, whose colonies are perennial, often taking three or more years to reach maturity, and thus having a longer lag time. Heavy grazing might also have more of an impact on ants, as colony-founding queens often seek areas of loose, bare soil rather than compacted soil in which to dig their incipient nests (J. C. Trager, *personal observation*).

Second, patch-burn grazing failed to generate among-patch heterogeneity in vegetation structure, thus vegetation structure of patch-burn graze tracts did not differ from that of graze-and-burn tracts (McGranahan 2011). Without the structural heterogeneity that is so important to insect diversity (Tscharntke and Greiler 1995), our implementation of patch-burn grazing failed to deliver the anticipated increase in diversity. Elsewhere, patch-burn grazing under moderate stocking has generated structural variation among patches (Fuhlendorf and Engle 2004, Winter et al., *in press*). In our patch-burn graze tracts, stocking rate may have been excessive, so that cattle were obliged to forage intensively on all patch-types, rather than focusing on the recently burned patches.

Our prediction that land-use legacies would

have significant effects on insect abundance and diversity was supported, but the patterns of response varied across the three insect groups. Land-use legacy variables such as grazing history, remnant history, fire history, and pre-treatment vegetation characteristics had numerous significant effects on ants, but fewer effects on butterfly or leaf beetle diversity or richness. In addition, the pre-treatment vegetation variables that were significantly correlated with insect abundance, richness, and diversity varied across taxonomic groups.

Ants exhibited higher richness and diversity in remnants and tracts with higher vegetation as compared to reconstructed grasslands and tracts with shorter vegetation. They also had lower Simpson diversity in tracts with a history of grazing. We speculate that ants were more affected by legacies in part because of the lower complexity of the ant dataset. Over 80% of the ants captured were *Formica montana*, therefore responses of ants to predictor variables were due in large part to a response of *F. montana*. *F. montana* is behaviorally dominant (Henderson et al. 1989), defending their above-ground nests from cows as well as other ant species. They are also numerically dominant (Trager 1998, Henderson et al. 1989) in prairies of central North America. We hypothesize that the lower richness and diversity of ants in grassland reconstructions is due to *F. montana* dominance. A lower abundance of *F. montana* in 2009 may have led to increased survival and fecundity of other ant species, particularly opportunist species, and thus an increase in ant diversity that year. As grassland reconstructions age, and habitat conditions become less suitable for *F. montana*, we predict that ant species richness will increase as other species colonize the reconstructions.

In contrast to ants, which are predacious and respond to prey availability, butterfly and leaf beetle communities of central North American grasslands have no analogous social hierarchy of species (and have no species that is numerically dominant), so we expected that their responses would be driven more by pre-treatment vegetation structure and diversity. A number of studies have found positive correlations between invertebrate diversity and plant diversity (Crisp et al. 1998, Stoner and Joern 2004), and Collinge et al. (2003) found differences in butterfly species richness among grassland types. In our system, butterfly abundance and diversity showed few significant responses to treatment or to land-use legacies beyond the positive association with pre-treatment litter cover. This legacy effect makes sense given that litter is an especially important habitat component for butterflies (Vogel et al. 2010). However, ordination provided additional insights by showing a clear separation between habitat-specialist species and habitat-generalist species. Of the four species (*Cercyonis pegala*, *Danaus plexippus*, *Lycaena hyllus*, and *Speyeria idalia*) associated with tracts having higher pre-treatment proportion of native cover and forb cover, all except *D. plexippus* have been designated as habitat specialists (i.e., grassland specialists) in prior studies (e.g., Panzer et al. 1995, Shepherd and Debinski 2005, Vogel et al. 2010). And although *D. plexippus* uses a wide variety of habitats when considering its entire range, we suspect its association with higher pre-treatment proportion of native plant cover is due to its dependence on native forbs (*Asclepias* spp.) as hosts.

Leaf beetles showed what might be the most predictable response of a group of host plant specialist insects to grassland characteristics. In contrast to ants, leaf beetles responded positively in terms of species richness and Shannon diversity to the pre-treatment proportion of native plant cover. We were surprised that leaf beetle richness and diversity did not respond to pre-treatment time since fire, but Hall and Barney (2011) found no significant effect of prescribed burns on species richness of leaf beetles or vegetation in several state nature preserves in Kentucky. Leaf beetle abundance did respond negatively to increased time since fire. This may be linked to the beneficial effects of fire in reducing dead plant biomass and promoting new plant growth (Glenn-Lewin et al. 1990) which can enhance food quality and availability for herbivorous insects (Tscharntke and Greiler 1995).

There were strong effects of year on all three taxa, which is not surprising, as populations of many insect species fluctuate widely from year to year (Andrewartha and Birch 1954). However, the three taxa were not synchronous in their fluctuations in abundance, richness and diversity (e.g., while butterfly abundance was high in 2008,

leaf beetle abundance was quite low). Some of the common butterfly species (*Colias philodice* and *Cupido comyntas*) suffered large population declines in 2009 (R. A. Moranz, *personal observation*). Initially, we suspected that fire was the cause, as most of our burn-only tracts and all of our graze-and-burn tracts were burned spring 2009. However, *C. philodice* and *C. comyntas* declined irrespective of treatment, including responses in tracts that were patch-burn grazed (thus receive approximately the same amount of prescribed fire each year). This suggests that some other factor (bad winter weather, disease outbreak, etc.) operating at the regional level was the cause of the declines.

In summary, land-use legacies and their associated pre-treatment vegetation conditions had significant effects on ants, butterflies and leaf beetles, but they did not have equivalent effects across taxa as measured by abundance, richness, or diversity. This is an important finding because managers might otherwise assume that all insects would respond in similar ways to land-use legacies. Others have found that cross-taxonomic comparisons can reveal disparities in richness patterns relative to habitat types or locations of diversity hotspots, meaning that one taxon cannot serve as a surrogate for another (e.g., Prendergast et al. 1993, Su et al. 2004, Davis et al. 2008). If our goal is conservation of all of these taxa, it is imperative to know that ants, butterflies, and leaf beetles are each responding to different components of land-use legacies. Virtually all grassland restoration projects are influenced by some type of land-use legacy, yet rarely are such legacies taken into consideration when evaluating restoration success. Whether these legacies are acknowledged or not, they may be having significant effects—even more significant than the current management being applied.

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SUPPLEMENTAL MATERIAL
APPENDIX A

Table A1. Characteristics of study tracts in the Grand River Grasslands of Iowa and Missouri.

Treatment	Tract name	Remnant history	Grazing history (2003–2005)	Previous pre-treatment fire	Tract area (ha)
Burn-only	Kellerton Tauke	Prairie restoration†	None	2003	32.4
Burn-only	Pawnee	Prairie remnant	None	2005	21.8
Burn-only	Richardson	Prairie remnant	None	1994 or earlier	15.6
Burn-only	Ringgold North	Prairie remnant	None	2004	15.4
Graze-and-burn	Gilleland	Prairie remnant	Cattle grazing	1994 or earlier	31.2
Graze-and-burn	Lee Trail Road	Prairie remnant	None	2004	34.0
Graze-and-burn	Pyland West	Prairie remnant	Cattle grazing	1994 or earlier	17.8
Graze-and-burn	Sterner	Prairie restoration†	None	1994 or earlier	32.4
Patch-burn graze	Ringgold South	Prairie remnant	Cattle grazing	2003	32.4
Patch-burn graze	Kellerton North	Prairie restoration†	None	2004	32.4
Patch-burn graze	Pyland North	Prairie remnant	Cattle grazing	1994 or earlier	25.3
Patch-burn graze	Pyland South	Prairie remnant	Cattle grazing	1994 or earlier	22.7

† Prairie restorations were restored from croplands between 1980 and 2004.

APPENDIX B

Table B1. Codes for ant scientific names used in community ordination (Fig. 3).

Code	Scientific name
CAAM	*Camponotus americanus*
FOEX	*Formica exsectoides*
FOIN	*Formica incerta*
FOMO	*Formica montana*
FOSU	*Formica subsericea*
LAAL	*Lasius alienus*
LANE	*Lasius neoniger*
MOMI	*Monomorium minimum*
MYAM	*Myrmica americana*
SOMO	*Solenopsis molesta*
TASE	*Tapinoma sessile*
TEAM	*Temnothorax ambiguus*
TEPE	*Temnothorax pergandei*

APPENDIX C

Table C1. Codes for butterfly scientific names used in community ordination (Fig. 4).

Code	Scientific name
BOBE	*Boloria bellona*
CENE	*Celastrina neglecta*
CEPE	*Cercyonis pegala*
CHGO	*Chlosyne gorgone*
COEU	*Colias eurytheme*
COPH	*Colias philodice*
CUCO	*Cupido comyntas*
DAPL	*Danaus plexippus*
EPCL	*Epargyreus clarus*
JUCO	*Junonia coenia*
LYDI	*Lycaena dione*
LYHY	*Lycaena hyllus*
PAPO	*Papilio polyxenes*
PHTH	*Phyciodes tharos*
PIRA	*Pieris rapae*
POOR	*Polites origenes*
POPE	*Polites peckius*
POTH	*Polites themistocles*
POPR	*Pontia protodice*
SATI	*Satyrium titus*
SPCY	*Speyeria cybele*
SPID	*Speyeria idalia*
THLI	*Thymelicus lineola*
VAAT	*Vanessa atalanta*
VACA	*Vanessa cardui*
VAVI	*Vanessa virginiensis*

APPENDIX D

Table D1. Codes for leaf beetle scientific names used in leaf beetle community ordination (Fig. 5).

Code	Scientific name
ANLA	*Anomoea laticlavia*
BALI	*Bassareus lituratus*
BRMA	*Brachypnoea margaretae*
CATH	*Capraita thyamoides*
CETR	*Cerotoma trifurcata*
CHSP	*Chaetocnema* spp.
COBR	*Colaspis brunnea*
CRVE	*Cryptocephalus venustus*
DIBA	*Diabrotica barberi*
DICR	*Diabrotica cristata*
DIUN	*Diabrotica undecimpunctata*
EPSP	*Epitrix* spp.
EXCA	*Exema canadensis*
GLSP	*Glyptina spuria*
LESA	*Lexiphanes saponatus*
LOSP	*Longitarsus* sp.
OPAM	*Ophraella americana*
OPCO	*Ophraella communa*
OPCR	*Ophraella cribrata*
ORCO	*Orthaltica copalina*
PAAT	*Pachybrachis atomarius*
PAOT	*Pachybrachis othonus*
PASE	*Paria sexnotata*
PATH	*Paria thoracica*
PHCR	*Phyllotreta cruciferae*
PHZI	*Phyllotreta zimmermani*
RHSP	*Rhabdopterus* sp.
TRVI	*Trirhabda virgata*
ZYSU	*Zygogramma suturalis*

esa

ECOSPHERE

A cross-taxonomic comparison of insect responses to grassland management and land-use legacies

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Abstract. Many species of plants and animals associated with grasslands are rare or declining due to habitat loss and degradation. Although grassland plants and insects evolved in the context of both grazing and fire, the appropriate use of grazing and fire has been debated among those concerned with protecting insect communities. We established an experiment to test insect responses to three grassland management treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle), (2) graze-and-burn (burning of entire tract with free access by cattle), and (3) burn-only. Because we expected that land-use legacies could also affect insect abundance and diversity, we evaluated effects of time since fire, grazing history, remnant history (remnant or reconstructed grassland) and pre-treatment vegetation characteristics, which were assumed to be a legacy of prior land-use. Butterflies (Lepidoptera), ants (Hymenoptera: Formicidae), and leaf beetles (Coleoptera: Chrysomelidae) were surveyed for three years to compare their responses to each of these treatments as measured by abundance, richness and species diversity. Each of these taxa is relatively diverse and was expected to have the potential to have strong negative responses to grazing and burning, but we predicted more positive responses to patch-burn grazing. Our results showed that land-use legacies affected insect abundance, richness and diversity, but treatments did not. Ant abundance was lower in tracts with a history of heavy grazing. Ant species richness was positively associated with pre-treatment time since fire and vegetation height and negatively associated with pre-treatment proportion native plant cover. Butterfly abundance was positively associated with pre-treatment litter cover. Leaf beetle diversity was positively associated with pre-treatment native plant cover, and leaf beetle abundance was negatively associated with time since fire. Our results indicate that land-use legacies can exert more influence on grassland insect community composition than current management, but the particular aspects of these land-use legacies that are important vary across insect taxa. The implications of these finding are that (1) land-use legacies should garner more attention in grassland management and (2) conservation of grassland insect communities will be improved by taxon-specific analysis of land-use legacy variables.

Key words: burning; butterflies; Chrysomelidae; Formicidae; grassland; grazing; insect diversity; Iowa; land-use legacy; Lepidoptera; Missouri; tallgrass prairie.

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Introduction

Managing and restoring grassland ecosystems for insect communities has been a topic of heated debate for the past few decades, and this is particularly true in the tallgrass prairie ecoregion of the U.S. The use of fire is contested among those concerned with protecting insect communities (Swengel 1998, Panzer and Schwartz 2000, Cook and Holt 2006), and concerns have been raised as to the compatibility of burning smaller grassland tracts relative to the conservation of insect populations within these tracts (Panzer 2002). Burning can greatly influence the presence-absence of arthropod species on a particular grassland tract, and species differ in their tolerances for fire (Warren et al. 1987, Swengel 1996). In addition, the time since fire can influence the species present (Reed 1997). Many insect species decline immediately after a burn (Swengel 2001) while other species increase (Gibson et al. 1993, Larsen and Work 2003, Moranz 2010), and the trajectory of abundance relative to time since burn can vary among species even within the same taxonomic group (Vogel et al. 2010).

Grazing, like fire, can affect the species abundance and diversity of grassland fauna (Andresen et al. 1990, Sutter and Ritchison 2005, Warui et al. 2005) and flora (Towne et al. 2005), and controversies have ensued regarding the potential impacts on insects. Grazing sometimes reduces grassland insect diversity (e.g., Stoner and Joern 2004), even in areas where it has little effect on the plant community (Milchunas et al. 1998), yet in other locations increases insect species richness and Shannon diversity (Joern 2005). The intensity of grazing can influence the direction of the insect response. For example, insect species richness was greater in grasslands with low-intensity grazing than those with high-intensity grazing (Kruess and Tscharntke 2002). Ants have been less extensively studied in grasslands, but in Argentine subtropical forest, ant community composition varied along a gradient of grazing intensity (Bestelmeyer and Wiens 1996). Ant species were distributed based on their preference for litter versus bare ground; both of these variables were affected by grazing, but can also be altered by burning.

Patch-burn grazing is a management approach that combines both fire and grazing and has potential for insect conservation because it creates heterogeneity in both the spatial and temporal patterns of grazing and burning (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Whereas uniform application of either grazing or fire can simplify the landscape, different levels of grazing creates habitat heterogeneity which can support a more diverse set of invertebrate species (Tscharntke and Greiler 1995, Swengel 2001). Patch-burn grazing involves subdividing a pasture into sections which are burned sequentially over multiple years. Large ungulates focus their grazing on the recently burned patches (Coppedge and Shaw 1998, Vermeire et al. 2004), creating a mosaic of (1) heavily grazed/recently burned patches, (2) patches that were burned six to 18 months earlier and are dominated by forbs after the ungulates have moved on to more recently burned patches, and (3) patches dominated by grass and senesced vegetation. Engle et al. (2008) found that the increased habitat heterogeneity generated by patch-burn grazing was reflected in increased heterogeneity of insect biomass compared to pastures under traditional homogeneity management.

However, in addition to current management, many grasslands are influenced by legacies of prior land-use (Burke et al. 1989, Trimble 1999). Plowing, grazing, and fire can leave immediate effects as well as enduring consequences on ecosystem structure and function for centuries after the processes have been operative (Foster et al. 2003). Land-use legacies can be measured via abiotic properties of the ecosystem (e.g., soil carbon, nitrogen content, soil compaction), as well as biotic components (e.g., current plant or animal community composition). It is often difficult to determine the history of land use, but this history can be important when evaluating grassland restoration success.

To better understand the responses of invertebrate communities to fire and/or grazing, a variety of investigators have quantified invertebrate community responses before and after disturbances (Nekola 2002, Larsen and Work 2003, Engle et al. 2008, Doxon et al. 2011). Due to taxonomic challenges, these responses are often quantified at the order or family level. Although these assessments provide important information, the interpretation of the results can be challenging because of the diversity of life history traits within a family (which may include herbivores, predators, or decomposers and species with life stages that include belowground as well as aboveground activity). Alternatively, much of the research that has been done at the species level to assess responses has focused on a single family or order.

Here we describe the results of an experimental grassland management project that compared abundance, species richness, and diversity responses of ants (Order Hymenoptera, Family Formicidae), butterflies (Order Lepidoptera), and leaf beetles (Order Coleoptera, Family Chrysomelidae) to three grassland treatments: burn-only, graze-and-burn, and patch-burn graze. These taxa are relatively diverse in grassland ecosystems and were expected to respond strongly to grazing, burning, or the combination thereof. Trager (1998) argues that the sheer biomass of ants compared with other insect families justifies research concerning ants. Additionally, ants often serve as ecosystem engineers by altering habitat through burrowing and foraging (Jones et al. 1994, Wagner et al. 2004) and have been shown to respond to anthropogenic change across a wide range of habitats (e.g., Majer and Nichols 1998, Bestelmeyer and Wiens 2001). Butterflies are excellent subjects for ecological management studies because they are relatively easy to identify in the field and can be highly responsive to disturbance via direct as well as indirect effects (Waltz and Covington 2004, Nelson 2007). Chrysomelid (leaf) beetles have been less extensively examined in grassland ecosystems, but are a diverse group of herbivores, and, like butterflies, many species have specialized associations with host plants (Clark et al. 2004, Barney and Hall 2011).

All three of these insect taxa could be expected to have strong responses to burning, grazing, and vegetative composition and structure due to their dependence on vegetation for food and habitat as well as the importance of bare ground or litter for nesting and overwintering habitat. In addition, there is value in cross-taxonomic comparison of these responses to determine whether a broader group of insects is responding similarly to disturbance patterns and/or habitat characteristics. With that in mind, we tested for effects of treatment (burn-only, graze-and-burn, and patch-burn graze) on abundance, richness, and diversity of each taxon, while simultaneously testing for effects of pre-treatment covariates, including land-use history variables (grazing history, remnant history [i.e. remnant versus reconstructed grassland]), fire history, and pre-treatment vegetation variables (i.e., composition and structure). The vegetation present at the beginning of our study is in fact the legacy of prior land use (McGranahan 2008, McGranahan 2011) and was expected to affect insect community richness and diversity patterns. We made the following predictions:

1. Patch-burn grazed tracts will have higher species richness and diversity compared to tracts managed using more traditional techniques (i.e., graze-and-burn and burn-only tracts) due to non-burned refugia, spatial heterogeneity of grazing pressure, and increased structural heterogeneity of the vegetation.
2. Prior land use (plowing, heavy grazing by cattle, and burning) will have left legacies that affect abundance, richness, and diversity of each of the three taxa (ants, leaf beetles and butterflies). Specifically, tracts that were plowed and later reconstructed, and tracts with a history of heavy grazing will have lower richness and diversity than grassland remnants and those that lacked a history of heavy grazing. Tracts with longer pre-treatment time since fire will have higher diversity and abundance of all three insect taxa.
3. Variation in pre-treatment vegetation characteristics (e.g., proportion native plant cover) that are legacies of land-use history will affect abundance and diversity of each of the three insect taxa, but these patterns may vary across the taxonomic groups

based upon habitat preferences for nest sites (ants), overwintering sites (butterflies), and species-specific plant use (all three taxa).

Methods

Study tracts

In 2006, we selected 12 tracts for a controlled experiment to test the effects of fire and grazing treatments on vegetation structure, plant community composition, and terrestrial insect community composition in the Grand River Grasslands of southern Iowa and northern Missouri, USA (Appendix A). The tracts, which ranged in size from 15 to 34 ha, occurred within a mixture of private and public grasslands. They were allocated to one of three treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle, $N = 4$), (2) graze-and-burn (burning of entire tract with free access by cattle, $N = 4$), and (3) burn-only (burning of entire tract with no grazing, $N = 4$). From 2007 through 2009, tracts receiving the first two treatments were stocked with cattle at about 3.4 animal unit months per ha between May 1 and October 1. Each tract was divided into three patches of approximate equal area. In patch-burn graze tracts, natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries to the extent possible. Each year, a different patch within each patch-burn graze tract was burned in early spring (mid-March). Tracts in the burn-only and graze-and-burn treatments were burned in their entirety in spring 2009, except for one burn-only tract, which was burned in spring 2008. Thus, the fire-return interval was the same across all three treatments.

Land-use history was classified in terms of remnant history as well as fire and grazing history. Remnants were defined as grassland tracts that had never been plowed, whereas reconstructed grasslands were planted from seed in bare soil. Pre-treatment time since fire denoted the number of years since fire had been applied to each tract as of 2006 (values ranged from 0 to 15 years). Grazing history was classified as either having a history of severe grazing or not. Although some of the tracts had long histories of severe grazing, we defined our pre-treatment legacies in terms of the previous three years (2003–2005) for consistency in this analysis. The land-use history of each tract was determined by interviewing landowners and governmental land managers who owned/managed the tracts.

Vegetation sampling

Pre-treatment vegetation variables were used as covariates to enable us to separate treatment from legacy effects. Pre-treatment vegetation data were collected in 2006 at the transect-level to describe plant community composition, and at the patch-level to describe plant composition and structure. Plant community composition was sampled twice during the summer season and measured at the species level in two permanently-marked Whittaker plots (Stohlgren et al. 1995) per patch (i.e., $N = 6$ Whittaker plots per tract) as described in McGranahan (2011). The canopy cover value for each species was the maximum canopy cover value observed. From Whittaker plot data, we calculated the proportion of native plant canopy cover in each patch, using the following equation: proportion native plant cover = total native plant canopy cover/(total native plant canopy cover + total exotic plant canopy cover).

During July of 2006 we measured pre-treatment plant functional group composition and vegetation structure in thirty 0.5-m^2 quadrats that were placed systematically within each patch as described in Pillsbury et al. (2011). Variables measured included Robel vegetation height (Robel et al. 1970), percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum* (Schreb.) S.J. Darbyshire (tall fescue). Cover measurements used the following cover classes: 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100% (Daubenmire 1959). Center points of each cover class were averaged within each patch ($N = 30$ quadrats/patch) and tract ($N = 90$ quadrats/tract).

Sweep net sampling

Sweep net surveys of terrestrial invertebrates were conducted in each tract twice per year during the periods of major emergence (June to early July and mid-July to early August) from 2007–2009. Surveys were conducted along 50-m transects parallel to the eastern edge of each

Whittaker plot with a starting point 10 m east of the north-center coordinate of each plot, resulting in 12 samples per tract per year (2 transects per patch × 3 patches per tract × 2 sampling periods per year). Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds. Surveys were conducted by a single individual walking south along each transect at a constant pace, holding a net with both hands with the net handle directed forward and the net opening pointed sideways. The net was swept at a constant pace from side to side 40 times, where one sweep includes the complete back and forth swing in both directions, as the individual traveled the transect. Completing 40 sweeps was preferred to traveling exactly 50 m to maintain constant effort. Insects were carefully transferred from the net to a plastic zip lock bag at the completion of each transect and frozen until they could be sorted. Due to the greater than expected labor costs of identifying insects, only samples from each patch's northern transect were identified, resulting in six identified samples per tract per year. Samples from each patch's southern transect remain frozen for future processing if funding permits.

Sweep net samples were sorted to family level, preserved in ethanol in vials categorized by tract, replicate, and date, and stored until they could be later identified to species. L. Winkler, with the assistance of J. Trager, identified ant species. R. Barney identified the chrysomelid leaf beetles.

Butterfly sampling

Butterflies were sampled via Pollard walk transects (Pollard and Yates 1993) twice per year from 2007–2009. Sampling was spaced temporally to cover the major emergence periods (June to early July and mid-July to early August). One 100 × 5-m transect was established parallel to the west side of each Whittaker vegetation sampling plot, with a starting point 10 m west of the north-center coordinate of the plot, resulting in 12 samples per tract per year (2 transects per patch × 3 patches per tract × 2 sampling periods per year). During butterfly sampling, an observer walked the transect at a steady pace (~10 m/min) and recorded data on butterflies seen within the 5 m × 5 m area in front of the observer (extending 2.5 m to each side of the transect, and 5 m forward). Each butterfly was identified to the species level. Specimens that could not be identified in the field were captured and identified in our lab. Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds.

Data analysis

Insect count data from the June and July sampling periods were added together, so that a single value of each response variable was obtained for each transect each year. For each of three major taxa, we calculated four response variables: abundance, species richness, Shannon diversity, and Simpson diversity. Abundance was defined here as the total number of individuals of each taxonomic group (butterflies, ants, or leaf beetles) found per transect. Species richness was calculated as the number of unique species found per transect. Shannon diversity was calculated as $H = -\sum(p_i \ln(p_i))$ and Simpson diversity was calculated as $D = 1 - \sum p_i 2$, where p_i is the percentage of ith species and ln is the natural log. Shannon diversity is a measure of species evenness, while Simpson diversity is a measure of species dominance (Magurran 2004). Due to the difference in total samples available, for butterflies, response variables were calculated for two transects per patch per year, whereas for ants and leaf beetles, response variables were calculated for one transect per patch per year.

Univariate data analysis.—We performed mixed model analysis of covariance using the statistical software package SAS version 9.2 (SAS Institute 2008) to test for effects of treatment and year on response variables for our three focal taxa after accounting for the influence of pre-treatment covariates. We viewed plots of residuals versus fitted values. If residuals failed to exhibit an approximately normal distribution, analyses were re-run with transformed response variables. Values of pre-treatment covariates were obtained in 2006. Before performing analysis of covariance, we reviewed the grassland insect literature to select a list of potential variables to serve as covariates. Then, we tested for correlations among those vegetation variables; when correlation coefficients were 0.70 or greater, the variable more likely to be associated with insect density (based

on our literature review) was retained as a covariate whereas the other was excluded to reduce multicollinearity. Pre-treatment covariates entered in all analyses of covariance included: grazing history, remnant history, time since fire, proportion of native plant cover, forb cover, Robel vegetation height, litter cover, and the cover of bare ground. Backward elimination was performed to remove insignificant covariates from each analysis of covariance, with $\alpha = 0.05$ used as criterion for retaining each covariate. When analysis of covariance indicated a significant effect of treatment, or a significant treatment by year interaction, we used differences of least squares means as our multiple comparison procedure.

Multivariate data analysis.—We used nonmetric multidimensional scaling (NMDS) to describe separately the structure of the ant, butterfly, and leaf beetle communities. NMDS is an unconstrained, distance-based ordination technique in which the distance between samples in ordination space corresponds to the similarity in community structure among samples. Ordinations were performed using VEGAN (Oksanen 2009), a package of community analysis functions for the statistical software R (R Development Core Team 2010). In order to avoid spurious results, species occurring in only one transect were not included in the ordinations. Bray-Curtis distance was used as the measure of dissimilarity among grassland transects.

For all ordinations, transect-level abundance data from 2007–2009 were plotted together, i.e., each point on the ordination represents community composition of a transect in a particular year. Thus, the vectors that describe the insect responses to vegetation variables represent the composite response across all three years. Subsequently, we tested for correlations between ordination axis scores and values of 11 pre-treatment vegetation variables derived from the same Whittaker plot locations: proportion of native plant cover, plant species richness, Robel vegetation height, percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum*. Vegetation variables significantly correlated with one or more ordination axes at $\alpha \leq 0.05$ were plotted as vectors.

Results

Over three years, the numbers of species and total individuals collected were as follows: ants: 14 species and 5101 individuals; butterflies: 33 species and 2048 individuals; leaf beetles: 44 species and 1189 individuals. Fig. 1 presents tract-level patterns of abundance (Fig. 1A), richness (Fig. 1B), Shannon diversity (Fig. 1C), and Simpson diversity (Fig. 1D) for each treatment, whereas Fig. 2 represents tract-level patterns of abundance and richness relative to grazing history and remnant history (with graphs of diversity indices omitted for simplicity's sake). However, the statistical results we wish to emphasize are those of Table 1 because the ANCOVA results evaluate responses of transect-level abundance, richness, and diversity after accounting for the influence of covariates, which is a more accurate representation of the responses. Grassland management treatments had no main effects on any of the four response variables (abundance, species richness, Shannon diversity and Simpson diversity) measured for each taxon, and had interactive effects (with year) only on butterfly abundance (Table 1). Because treatment showed no significant main effects, we present ordinations of each of the communities superimposed with vectors defining significant pre-treatment vegetation variables relative to species distributions but without designation of treatment type. Year affected response variables for each of the three taxa. Regarding significant year effects, we refer the reader to Table 1 and save further mention of this for the discussion.

Ants

Grasslands with a recent history (2003–2005) of grazing had fewer ants ($F = 7.75$, df = 1, 10, $P = 0.019$), than grasslands without such a history (Table 1, Fig. 2A). No other factors, including remnant history (Fig. 2C) affected ant abundance (Table 1). Ant species richness was influenced by three pre-treatment covariates (Table 1, Fig. 2B, D): remnant history (with remnants having greater species richness than reconstructed grasslands), proportion native cover (negative correlation), and Robel vegetation height (positive correlation). Remnant grasslands had greater Shannon diversity of ants than reconstructed

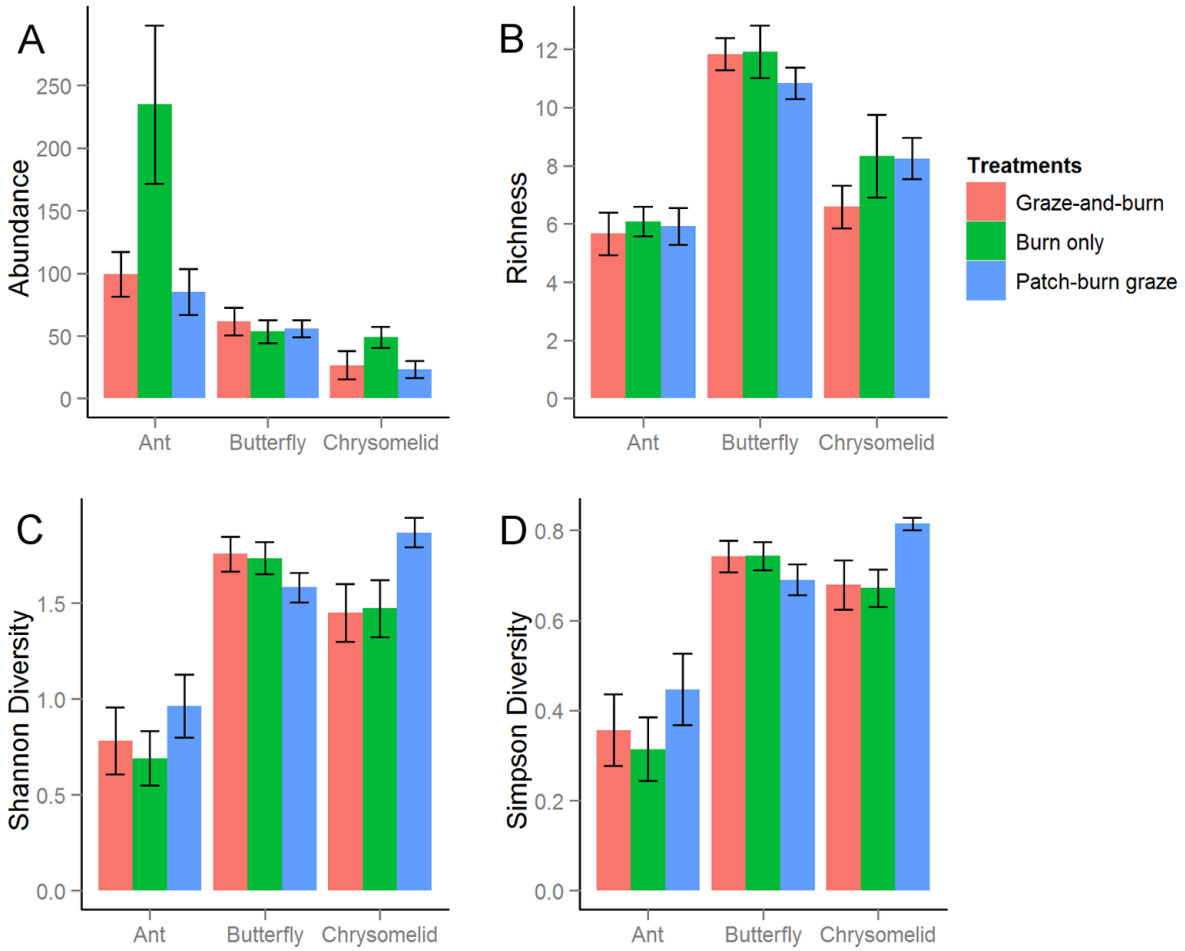

Fig. 1. Treatments compared for (A) abundance, (B) species richness, (C) Shannon diversity, and (D) Simpson diversity of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

grasslands ($P = 0.002$, Table 1). Three pre-treatment covariates were positively correlated with Shannon diversity: cover of bare ground, Robel vegetation height, and time since fire (Table 1). Several findings on Simpson diversity were consistent with those obtained on Shannon diversity: (1) ant diversity did not differ among treatments, (2) remnants had greater ant diversity than reconstructions ($P < 0.001$), and (3) Robel vegetation height was positively correlated with ant diversity ($P < 0.001$). However, two unique results were obtained using Simpson diversity. Tracts having a recent history of heavy grazing had lower ant diversity than tracts without that history ($P = 0.027$), and proportion of native cover was negatively correlated with ant diversity ($P = 0.002$).

Ordination of ant data (Fig. 3) showed that grasslands dominated by *Formica montana,* the most abundant ant species in our study (representing 81% of all ants captured), separated from grasslands with several less dominant species (*Camponotus americanus*, *Formica subsericea*, *F. exsectoides* and *Lasius alienus*). The ant community ordination was correlated with one vegetation variable: pre-treatment Robel vegetation height ($r^2 = 0.06$, $P = 0.025$).

Butterflies

Treatment and year interacted to affect butterfly abundance ($P = 0.029$) (Table 1): both grazing treatments exhibited high interannual variation

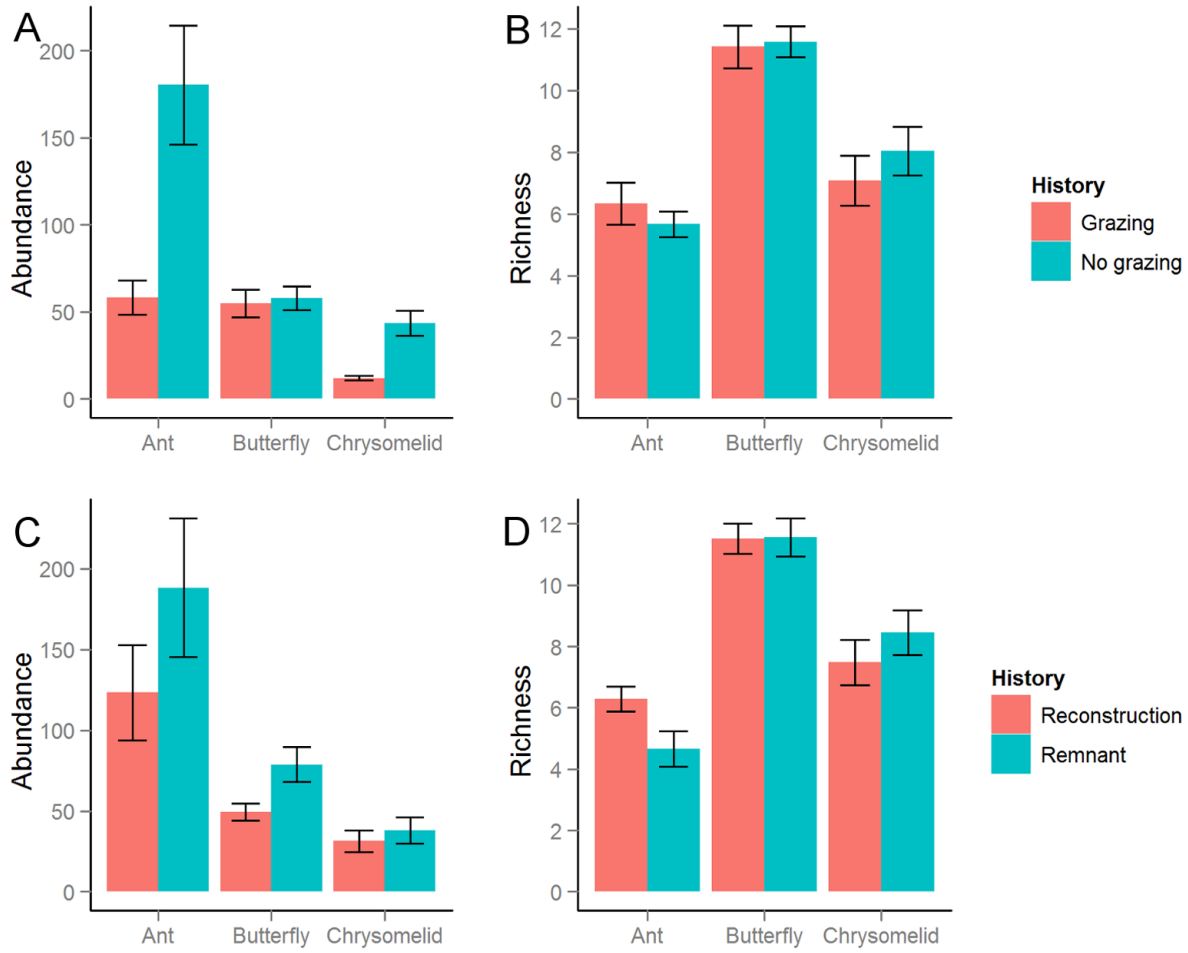

Fig. 2. Effects of grazing history on (A) abundance and (B) species richness, and effects of remnant history on (C) abundance and (D) species richness of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

in butterfly abundance ($P < 0.001$ for each treatment), whereas abundance did not vary among years in the burn-only treatment. Pre-treatment litter cover was positively associated with butterfly abundance ($P = 0.011$, Table 1). No pre-treatment covariates were associated with butterfly species richness, or with either diversity index (Shannon or Simpson) (Table 1, Fig. 2A–D). Ordination of butterfly community structure (Fig. 4) showed that three habitat specialists (*Cercyonis pegala*, *Lycaena hyllus* and *Speyeria idalia*) and one habitat generalist (*Danaus plexippus*) were associated with grasslands having greater pre-treatment proportion native cover ($r^2 = 0.41$, $P = 0.002$), forb cover ($r^2 = 0.20$, $P = 0.008$), and woody cover ($r^2 = 0.07$, $P = 0.012$). Species at the opposite end of the primary ordination axis included two exotic, habitat-generalist species (*Thymelicus lineola* and *Pieris rapae*) and three native, habitat-generalist species (*Cupido comyntas*, *Colias philodice*, and *Papilio polyxenes*) that were associated with pre-treatment values of cool season grass cover ($r^2 = 0.07$, $P = 0.06$) (Fig. 4).

Leaf beetles

Pre-treatment values of time since fire were negatively associated with leaf beetle abundance ($P = 0.01$) (Table 1). Pre-treatment values of proportion native cover were positively associated with leaf beetle species richness ($P = 0.018$) and Shannon diversity ($P = 0.022$), whereas no covariates were significant predictors of Simpson

Table 1. Associations between independent variables and insect response variables.

	Ants				Butterflies				Leaf beetles			
Independent variables	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM
Experimental variables												
Treatment												
Year			**	***	***	**			**	*	**	*
Treatment × Year					*							
Legacy variables												
Grazing history	−*			−*								
Remnant history		+*	+**	+***								
Time since fire			+*						-**			
Proportion native cover		−*		−**						+*	+*	
Forb cover												
Bare ground cover			+**									
Litter cover					+*							
Robel vegetation height		+***	+***	+***								

Notes: Legacy variables are covariate data from 2006. Response variables are based on data from 2007, 2008 and 2009, and are abbreviated as follows: AB = abundance, RIC = species richness, SHA = Shannon diversity, SIM = Simpson diversity. Blank cell indicates that independent variable was not a significant predictor of response variable. Asterisks indicate that independent variable was a significant predictor of response variable: * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$. Plus and minus signs indicate whether the relationship between variables was positive or negative. For the independent variable "grazing history" a minus sign indicates that grasslands with a recent history of grazing had lower values of response variable than grasslands without a recent history of grazing. For the independent variable "remnant history" a plus sign indicates that remnant grasslands had higher values of response variable than grassland reconstructions.

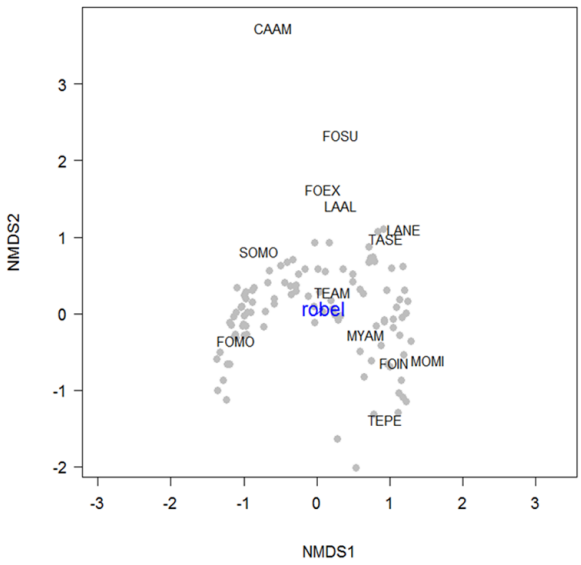

Fig. 3. Ant community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet, see Appendix B). Pre-treatment Robel vegetation height (robel) is significantly correlated with the ordination and is plotted as a vector to demonstrate its relationship to ant community composition.

diversity. Leaf beetle community structure (Fig. 5) was correlated with pre-treatment variables including proportion native plant cover ($r^2 = 0.50$, $P = 0.013$), warm season grass cover ($r^2 = 0.40$, $P = 0.024$), cool season grass cover ($r^2 = 0.26$, $P = 0.038$), and legume cover ($r^2 = 0.17$, $P = 0.025$). Some of the more common species of leaf beetles (e.g., *Zygogramma suturalis*, *Epitrix* spp., *Paria thoracica*, *Diabrotica barberi* and *D. undecimpunctata*) were widely separated in ordination space.

Discussion

The results of this research show that land-use legacies had far more influence on insect distribution and abundance patterns than currently imposed management treatments, even after three years of treatment implementation. Our prediction that patch-burn grazed tracts would have higher species richness and diversity of ants, butterflies, and leaf beetles than tracts managed for homogeneity was not supported by our results. In fact, this experiment showed few effects of burning and grazing treatments on invertebrate abundance, richness and diversity measures. These results contrast strongly with responses observed for grassland birds within the same tracts (Pillsbury et al. 2011).

We propose two hypotheses to explain this

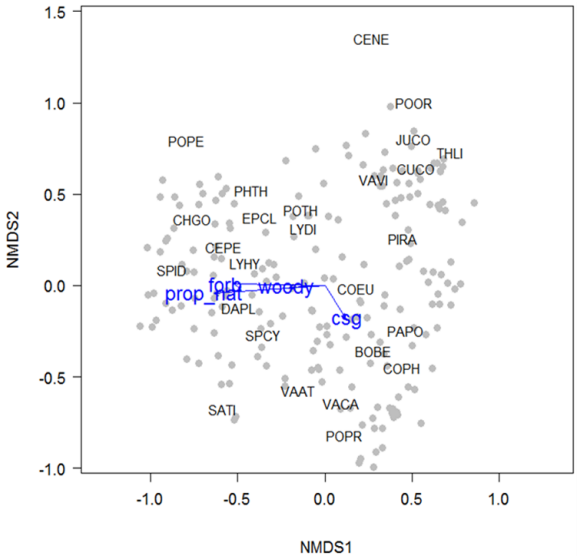

Fig. 4. Butterfly community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix C). Four pre-treatment vegetation variables significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with butterfly community composition: cool season grass cover (csg) woody plant cover (woody), forb cover (forb), and proportion of native plant cover (prop_nat).

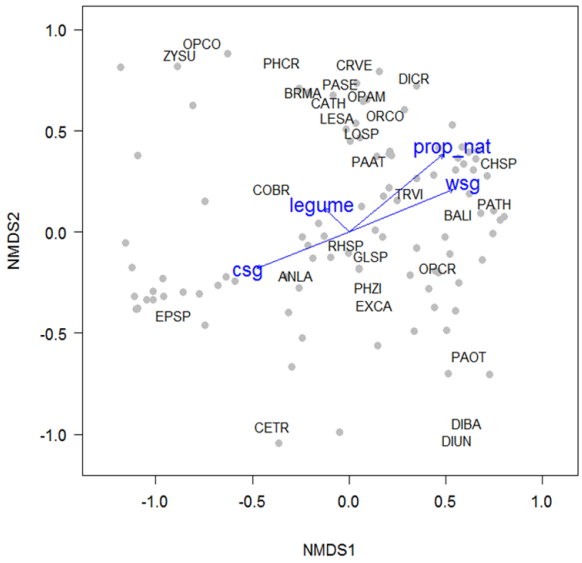

Fig. 5. Chrysomelid community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix D). Four pre-treatment vegetation variables that are significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with chrysomelid community composition. These variables are cool season grass cover (csg), legume cover (legume), proportion of native plant cover (prop_nat) and warm season grass cover (wsg).

unexpected outcome. First, for some taxa, particularly ants, legacies of previous land-use appear to have had significant impacts on determining local distribution and abundance. These legacies may have diminished our ability to observe treatment effects, and three years of these treatments are not enough to alter differences in abundance, diversity and composition that were established by heavy grazing. This might be especially so for ants, whose colonies are perennial, often taking three or more years to reach maturity, and thus having a longer lag time. Heavy grazing might also have more of an impact on ants, as colony-founding queens often seek areas of loose, bare soil rather than compacted soil in which to dig their incipient nests (J. C. Trager, *personal observation*).

Second, patch-burn grazing failed to generate among-patch heterogeneity in vegetation structure, thus vegetation structure of patch-burn graze tracts did not differ from that of graze-and-burn tracts (McGranahan 2011). Without the structural heterogeneity that is so important to insect diversity (Tscharntke and Greiler 1995), our implementation of patch-burn grazing failed to deliver the anticipated increase in diversity. Elsewhere, patch-burn grazing under moderate stocking has generated structural variation among patches (Fuhlendorf and Engle 2004, Winter et al., *in press*). In our patch-burn graze tracts, stocking rate may have been excessive, so that cattle were obliged to forage intensively on all patch-types, rather than focusing on the recently burned patches.

Our prediction that land-use legacies would

have significant effects on insect abundance and diversity was supported, but the patterns of response varied across the three insect groups. Land-use legacy variables such as grazing history, remnant history, fire history, and pre-treatment vegetation characteristics had numerous significant effects on ants, but fewer effects on butterfly or leaf beetle diversity or richness. In addition, the pre-treatment vegetation variables that were significantly correlated with insect abundance, richness, and diversity varied across taxonomic groups.

Ants exhibited higher richness and diversity in remnants and tracts with higher vegetation as compared to reconstructed grasslands and tracts with shorter vegetation. They also had lower Simpson diversity in tracts with a history of grazing. We speculate that ants were more affected by legacies in part because of the lower complexity of the ant dataset. Over 80% of the ants captured were *Formica montana*, therefore responses of ants to predictor variables were due in large part to a response of *F. montana*. *F. montana* is behaviorally dominant (Henderson et al. 1989), defending their above-ground nests from cows as well as other ant species. They are also numerically dominant (Trager 1998, Henderson et al. 1989) in prairies of central North America. We hypothesize that the lower richness and diversity of ants in grassland reconstructions is due to *F. montana* dominance. A lower abundance of *F. montana* in 2009 may have led to increased survival and fecundity of other ant species, particularly opportunist species, and thus an increase in ant diversity that year. As grassland reconstructions age, and habitat conditions become less suitable for *F. montana*, we predict that ant species richness will increase as other species colonize the reconstructions.

In contrast to ants, which are predacious and respond to prey availability, butterfly and leaf beetle communities of central North American grasslands have no analogous social hierarchy of species (and have no species that is numerically dominant), so we expected that their responses would be driven more by pre-treatment vegetation structure and diversity. A number of studies have found positive correlations between invertebrate diversity and plant diversity (Crisp et al. 1998, Stoner and Joern 2004), and Collinge et al. (2003) found differences in butterfly species richness among grassland types. In our system, butterfly abundance and diversity showed few significant responses to treatment or to land-use legacies beyond the positive association with pre-treatment litter cover. This legacy effect makes sense given that litter is an especially important habitat component for butterflies (Vogel et al. 2010). However, ordination provided additional insights by showing a clear separation between habitat-specialist species and habitat-generalist species. Of the four species (*Cercyonis pegala*, *Danaus plexippus*, *Lycaena hyllus*, and *Speyeria idalia*) associated with tracts having higher pre-treatment proportion of native cover and forb cover, all except *D. plexippus* have been designated as habitat specialists (i.e., grassland specialists) in prior studies (e.g., Panzer et al. 1995, Shepherd and Debinski 2005, Vogel et al. 2010). And although *D. plexippus* uses a wide variety of habitats when considering its entire range, we suspect its association with higher pre-treatment proportion of native plant cover is due to its dependence on native forbs (*Asclepias* spp.) as hosts.

Leaf beetles showed what might be the most predictable response of a group of host plant specialist insects to grassland characteristics. In contrast to ants, leaf beetles responded positively in terms of species richness and Shannon diversity to the pre-treatment proportion of native plant cover. We were surprised that leaf beetle richness and diversity did not respond to pre-treatment time since fire, but Hall and Barney (2011) found no significant effect of prescribed burns on species richness of leaf beetles or vegetation in several state nature preserves in Kentucky. Leaf beetle abundance did respond negatively to increased time since fire. This may be linked to the beneficial effects of fire in reducing dead plant biomass and promoting new plant growth (Glenn-Lewin et al. 1990) which can enhance food quality and availability for herbivorous insects (Tscharntke and Greiler 1995).

There were strong effects of year on all three taxa, which is not surprising, as populations of many insect species fluctuate widely from year to year (Andrewartha and Birch 1954). However, the three taxa were not synchronous in their fluctuations in abundance, richness and diversity (e.g., while butterfly abundance was high in 2008,

leaf beetle abundance was quite low). Some of the common butterfly species (*Colias philodice* and *Cupido comyntas*) suffered large population declines in 2009 (R. A. Moranz, *personal observation*). Initially, we suspected that fire was the cause, as most of our burn-only tracts and all of our graze-and-burn tracts were burned spring 2009. However, *C. philodice* and *C. comyntas* declined irrespective of treatment, including responses in tracts that were patch-burn grazed (thus receive approximately the same amount of prescribed fire each year). This suggests that some other factor (bad winter weather, disease outbreak, etc.) operating at the regional level was the cause of the declines.

In summary, land-use legacies and their associated pre-treatment vegetation conditions had significant effects on ants, butterflies and leaf beetles, but they did not have equivalent effects across taxa as measured by abundance, richness, or diversity. This is an important finding because managers might otherwise assume that all insects would respond in similar ways to land-use legacies. Others have found that cross-taxonomic comparisons can reveal disparities in richness patterns relative to habitat types or locations of diversity hotspots, meaning that one taxon cannot serve as a surrogate for another (e.g., Prendergast et al. 1993, Su et al. 2004, Davis et al. 2008). If our goal is conservation of all of these taxa, it is imperative to know that ants, butterflies, and leaf beetles are each responding to different components of land-use legacies. Virtually all grassland restoration projects are influenced by some type of land-use legacy, yet rarely are such legacies taken into consideration when evaluating restoration success. Whether these legacies are acknowledged or not, they may be having significant effects—even more significant than the current management being applied.

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SUPPLEMENTAL MATERIAL
APPENDIX A

Table A1. Characteristics of study tracts in the Grand River Grasslands of Iowa and Missouri.

Treatment	Tract name	Remnant history	Grazing history (2003–2005)	Previous pre-treatment fire	Tract area (ha)
Burn-only	Kellerton Tauke	Prairie restoration†	None	2003	32.4
Burn-only	Pawnee	Prairie remnant	None	2005	21.8
Burn-only	Richardson	Prairie remnant	None	1994 or earlier	15.6
Burn-only	Ringgold North	Prairie remnant	None	2004	15.4
Graze-and-burn	Gilleland	Prairie remnant	Cattle grazing	1994 or earlier	31.2
Graze-and-burn	Lee Trail Road	Prairie remnant	None	2004	34.0
Graze-and-burn	Pyland West	Prairie remnant	Cattle grazing	1994 or earlier	17.8
Graze-and-burn	Sterner	Prairie restoration†	None	1994 or earlier	32.4
Patch-burn graze	Ringgold South	Prairie remnant	Cattle grazing	2003	32.4
Patch-burn graze	Kellerton North	Prairie restoration†	None	2004	32.4
Patch-burn graze	Pyland North	Prairie remnant	Cattle grazing	1994 or earlier	25.3
Patch-burn graze	Pyland South	Prairie remnant	Cattle grazing	1994 or earlier	22.7

† Prairie restorations were restored from croplands between 1980 and 2004.

APPENDIX B

Table B1. Codes for ant scientific names used in community ordination (Fig. 3).

Code	Scientific name
CAAM	*Camponotus americanus*
FOEX	*Formica exsectoides*
FOIN	*Formica incerta*
FOMO	*Formica montana*
FOSU	*Formica subsericea*
LAAL	*Lasius alienus*
LANE	*Lasius neoniger*
MOMI	*Monomorium minimum*
MYAM	*Myrmica americana*
SOMO	*Solenopsis molesta*
TASE	*Tapinoma sessile*
TEAM	*Temnothorax ambiguus*
TEPE	*Temnothorax pergandei*

APPENDIX C

Table C1. Codes for butterfly scientific names used in community ordination (Fig. 4).

Code	Scientific name
BOBE	*Boloria bellona*
CENE	*Celastrina neglecta*
CEPE	*Cercyonis pegala*
CHGO	*Chlosyne gorgone*
COEU	*Colias eurytheme*
COPH	*Colias philodice*
CUCO	*Cupido comyntas*
DAPL	*Danaus plexippus*
EPCL	*Epargyreus clarus*
JUCO	*Junonia coenia*
LYDI	*Lycaena dione*
LYHY	*Lycaena hyllus*
PAPO	*Papilio polyxenes*
PHTH	*Phyciodes tharos*
PIRA	*Pieris rapae*
POOR	*Polites origenes*
POPE	*Polites peckius*
POTH	*Polites themistocles*
POPR	*Pontia protodice*
SATI	*Satyrium titus*
SPCY	*Speyeria cybele*
SPID	*Speyeria idalia*
THLI	*Thymelicus lineola*
VAAT	*Vanessa atalanta*
VACA	*Vanessa cardui*
VAVI	*Vanessa virginiensis*

APPENDIX D

Table D1. Codes for leaf beetle scientific names used in leaf beetle community ordination (Fig. 5).

Code	Scientific name
ANLA	*Anomoea laticlavia*
BALI	*Bassareus lituratus*
BRMA	*Brachypnoea margaretae*
CATH	*Capraita thyamoides*
CETR	*Cerotoma trifurcata*
CHSP	*Chaetocnema* spp.
COBR	*Colaspis brunnea*
CRVE	*Cryptocephalus venustus*
DIBA	*Diabrotica barberi*
DICR	*Diabrotica cristata*
DIUN	*Diabrotica undecimpunctata*
EPSP	*Epitrix* spp.
EXCA	*Exema canadensis*
GLSP	*Glyptina spuria*
LESA	*Lexiphanes saponatus*
LOSP	*Longitarsus* sp.
OPAM	*Ophraella americana*
OPCO	*Ophraella communa*
OPCR	*Ophraella cribrata*
ORCO	*Orthaltica copalina*
PAAT	*Pachybrachis atomarius*
PAOT	*Pachybrachis othonus*
PASE	*Paria sexnotata*
PATH	*Paria thoracica*
PHCR	*Phyllotreta cruciferae*
PHZI	*Phyllotreta zimmermani*
RHSP	*Rhabdopterus* sp.
TRVI	*Trirhabda virgata*
ZYSU	*Zygogramma suturalis*

esa

ECOSPHERE

Seasonal succession of pollinator floral resources in four types of grasslands

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Abstract. Pollinators are declining globally, and this decline in ecosystem services threatens the stability of agricultural and natural systems. Pollinators depend on a diversity of floral resources that are primarily found in uncultivated areas of agro-ecosystems such as grasslands. Seasonal succession (the seasonal changes that occur in community composition and structure) of floral resources is an essential consideration for pollinator conservation within agro-ecosystems. Different types of grasslands common within agricultural landscapes could be expected to differ in their seasonal succession of floral resources. Here we investigated how different types of grasslands important for pollinator conservation in the tallgrass prairie ecoregion (remnant prairies, reconstructed prairies, conservation grazed cattle pastures, and old fields) differ in their seasonal succession of floral resources by sampling the plant community every two weeks from 3 May through 4 October 2013. We found remnant prairies had greater richness of inflorescences when summed over the growing season, and that remnants were least similar to the other grassland types in terms of composition. Reconstructed prairies had high richness of inflorescences and exhibited the most similarity in composition to remnant prairies only during the middle of the growing season. Conservation grazed cattle pastures had more periods where turnover in composition from one survey to the next was low, indicated by the coefficient of variation in turnover throughout the season. Old fields had the lowest richness of inflorescences and were significantly different from reconstructed and remnant prairies.

Key words: agro-ecosystems; flowering phenology; resource diversity; restoration; tallgrass prairie.

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INTRODUCTION

In recent decades declines in pollinators have been observed both within the Midwestern United States (Grixti et al. 2009, Swengel et al. 2011) and globally (Biesmeijer et al. 2006, Potts et al. 2010). Mitigation of these losses requires the conservation of existing habitat, creation of new habitats, and development of management practices and conservation programs that increase pollinator resources on the landscape (Isaacs et al. 2008, Bennett and Gratton 2013). Grasslands are crucial for the conservation of pollinators in agricultural ecosystems (Öckinger and Smith 2007), because they provide nesting sites and floral resources. Given that the availability of floral resources is hypothesized to be the factor driving bee abundance and diversity in most landscapes (Roulston and Goodell 2011), the seasonal succession (the seasonal changes in community composition and structure) of these resources is an essential consideration for pollinator habitats in agricultural ecosystems (Corbet et al. 1991). However, floral resource availability

can vary among grassland types and can exhibit seasonal differences among grassland types (Parrish and Bazzaz 1979). Understanding how different grassland habitats contrast in their seasonal succession of floral resources will aid in understanding the utility of different grassland types for conservation of pollinators. It will also aid scientists and managers in developing best practices for grassland restoration and conservation.

Many pollinators depend upon floral resources to complete their life cycle (Abrol 2011, Wäckers and van Rijn 2012), and a diversity of floral resources is essential (Heinrich 2004, Tasei and Aupinel 2008, Alaux et al. 2010). The abundance, richness, and diversity of floral resources is correlated with the abundance and richness of butterflies (Shepherd and Debinski 2005) and diversity of bumble-bees (Hines and Hendrix 2005, Davis et al. 2008) in the tallgrass prairie, and similar patterns have been demonstrated in ecosystems throughout the world (Potts et al. 2003, Hegland and Boeke 2006, Holzschuh et al. 2007, Williams et al. 2012, Bennett and Gratton 2013). The seasonal succession of floral resources could be particularly relevant for the conservation of long-lived pollinators and pollinator colonies that forage throughout much of the growing season. For instance, landscapes that lack adequate floral resources during a portion of the growing season have been shown to negatively impact bumblebee numbers (Persson and Smith 2013) and colony growth (Williams et al. 2012).

Within the tallgrass prairie ecoregion, perennial grasslands are vital for providing native pollinators with the floral resources and nesting sites they require. In recent decades grassland habitats have declined throughout the Midwestern United States due to agricultural intensification and development (Wright and Wimberly 2013). In addition to typical prairie conservation and restoration projects, programs such as the U.S. Conservation Reserve Program, that provides farmers incentives to protect set-aside land, can bolster agro-ecosystems by providing habitat and resources for pollinators while still providing economic benefits to farmers (Vulliamy et al. 2006, Decourtye et al. 2010). Similarly, grazing initiatives that promote sustainable grazing practices, such as the U.S. Conservation of Private Grazing Land Program, can also benefit pollinators and other wildlife, and contribute to the long-term stability of agro-ecosystems.

Here we compare four types of grasslands with respect to their seasonal succession of floral resources: (1) remnant prairies, (2) reconstructed prairies, (3) conservation grazed pastures, and (4) old fields. In the Midwestern U.S., the conditions of each of these grasslands are described as follows: Remnant prairies best approximate the native tallgrass prairie community because these sites have retained a high proportion of native flora. Reconstructed prairies were formerly cultivated fields and have since been seeded with native prairie plant species. Conservation grazed cattle pastures are defined by having a low stocking rate ($\bar{x} = 2.6$ AUM/ha, SD = 0.95) and have either never been cultivated or have been cultivated for such a brief time in their past that they maintain some remnant flora. In our region, these sites were often grazed heavily in the past and are now dominated by exotic plant species that are common agricultural weeds in our region (e.g., *Trifolium pratense*, *Lotus corniculatus*, *Bromus inermis*, and *Schedonorus arundinaceus*). Finally, old fields are plant communities that arise naturally following cessation of agricultural practices and are typical of lands owned by absentee landowners and of some lands enrolled in conservation reserve programs, and also have a high proportion of exotic plant species.

Previous comparisons of the types of grasslands outlined above have found they differ in a number of characteristics. Remnant and reconstructed tallgrass prairie can differ in in terms of physical vegetation structure (Ammann and Nyberg 2005), productivity (Martin et al. 2005), as well as diversity of plants (Kindscher and Tieszen 1998, Martin et al. 2005, Polley et al. 2005), and invertebrates (Bomar 2001, Larsen and Work 2003, Shepherd and Debinski 2005, Nemec and Bragg 2008). Grasslands with high proportions of exotic species cover, such as our conservation grazed pastures and old fields, have also been shown to differ from remnant communities in terms of biodiversity, phenology, photosynthetic mode, productivity, and ecosystem services (Wilsey et al. 2009, 2011, Isbell and Wilsey 2011, Martin et al. 2014). Additionally, old fields and reconstructed prairies have been shown to differ in terms of butterfly diversity

and floral quality index (Farhat et al. 2014).

Our goal was to characterize patterns of seasonal succession of floral resources in these four different types of grasslands, and to test hypotheses defining the specific ways that they differed in their seasonal succession of floral resources. We predicted: (1) Remnant prairies would have the greatest richness of floral resources summed over the growing season, would have the greatest difference in composition compared to other grassland types, and would show the greatest stability as measured by turnover of floral resources throughout the growing season. (2) Reconstructed prairies would be the most similar to remnant prairies in terms of composition and diversity of floral resources but floral resources would be low in the beginning of the season and relatively high in the mid-season when many of the plant species favored in seeding projects tend to bloom. (3) Cattle pastures, which are dominated by long-flowering exotic forage species, would show the lowest amount of turnover in flower composition between each sampling period over the growing season. (4) Old fields would have the lowest richness of floral resources throughout the season and would be least similar to remnant prairies in terms of composition.

Methods

Our study sites were located in the Grand River Grasslands, a region covering over 28,000 ha in Ringgold County, Iowa, and Harrison County, Missouri, USA. We identified sites within the Grand River Grasslands that were characteristic of four types of grasslands essential for conservation in our region based upon communication with area land managers and current features of the plant communities. Grassland types and specifications for their designations are explained in the introduction section. A total of 16 sites were selected for this study with four sites in each of the four grassland types (Fig. 1, Table 1). Eight sites utilized previously established 100 m long butterfly transects (Debinski et al. 2011) for the plant survey transects; in the eight new sites, four randomly placed transects were established. Each transect ran north to south with some slight alterations to avoid barriers within the landscape (e.g., brush piles and drainage areas). The percent cover of native vegetation was estimated visually from 10 1×0.5 m quadrats along each transect (five quadrats on each side of the transect one meter from the transect line at 10, 30, 50, 70, and 90 m from the start of the transect; data presented in Table 1).

Inflorescences were sampled at two week intervals over 12 sampling rounds beginning 3 May and ending on 5 October 2013. Each sampling round was completed in 1–3 days. Inflorescences were counted by species along a 1 m swath along the east side of each 100 m transect. Inflorescences were characterized as the largest consistent floral unit among individuals within a species (e.g., compound umbels in Apiaceae and capitulums in Asteraceae), similar to the methods of Rotenberry (1990). For species that produce corymbs of inconsistent structure (e.g., *Asclepias tuberosa*, *Pycnanthemum* spp., and *Vernonia* spp.) the entire corymb on an individual flowering stem was counted as one inflorescence. Panicles were not considered the largest consistent unit for any species. All species were identified in the field using regional field guides. Some species were identified only to the genus level and are counted as an individual species in the analyses (i.e., *Cirsium*, *Erigeron*, *Fragaria*, *Lonicera*, *Plantago*, *Rubus*, *Vernonia*). Although pollinators are known to collect pollen from grass flowers, we did not count inflorescences for members of the Poales. We also acknowledge that pollinators derive nutrients from other sources besides flowers that we did not quantify here, which may include extrafloral nectaries, rotting fruit, sap, dung, carrion, and wet soil (Willemstein 1987). One site in the reconstruction category was hay-mowed in the beginning of August, so this site was eliminated from all following analyses that averaged data throughout the season.

To test for differences in the total number of inflorescences and flowering species over the sampling season, the total number of inflorescences was summed over all 12 sampling rounds for each transect, and species richness was calculated for each transect after abundances were summed. General Linear Mixed Models (GLMM) were used to test for differences among grassland types using the Poisson distribution (because data consisted of counts) with site as the

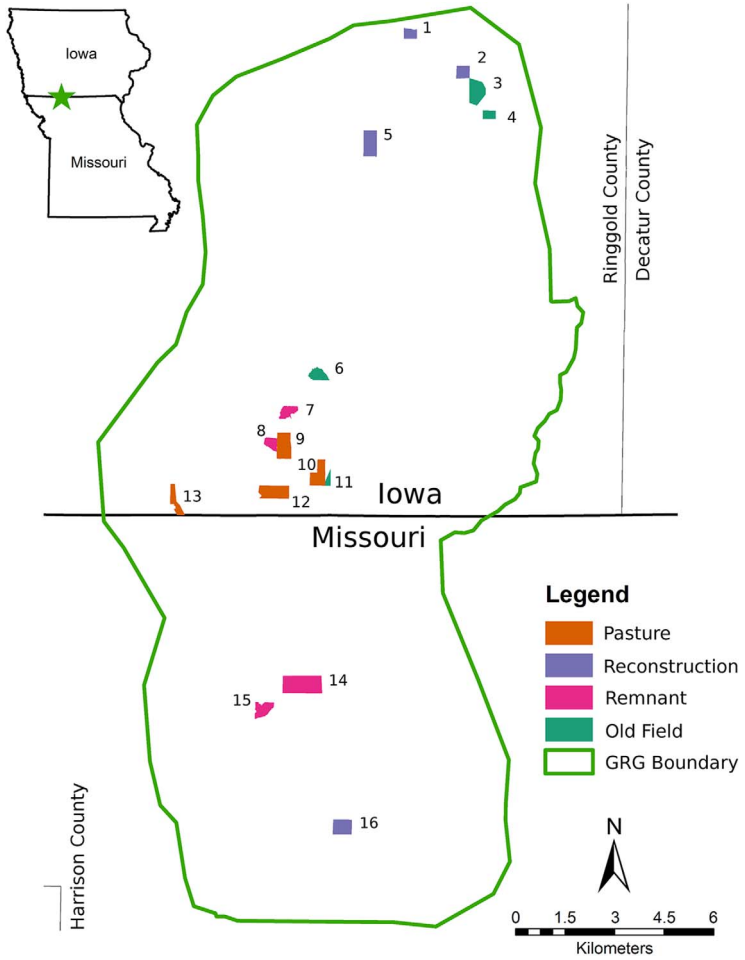

Fig. 1. Map depicting the 16 research sites in the Grand River Grasslands (GRG) of Ringgold county Iowa, and Harrison county Missouri. The thick horizontal black line is the Iowa/Missouri state border, thinner black lines are county borders. See Table 1 for details on each site.

random variable (to account for repeated measures within each site) using the nlme package (Pinheiro et al. 2013) in R (R Development Core Team 2010).

For seasonal changes in abundance of inflorescences and richness of flowering species we calculated the totals from each transect within each round. We tested for differences between grassland types within each round using GLMM with site as the random variable. To account for multiple comparisons we employed a Bonferroni correction ($p = 0.05/72 = 6.9 \times 10^{-4}$) to determine whether comparisons among grassland types within each of the sampling rounds were statistically significant.

Non-metric multidimensional scaling (NMDS) was used to observe seasonal changes in composition over time and compositional differences among grassland types. NMDS was chosen because this ordination technique has been shown to be more robust to the occurrence of rare species than other common ordination methods (Cao et al. 2001). To observe seasonal changes, species composition was averaged by each site within each round. For overall compositional differences, the total abundance of each species was calculated over all rounds for each transect and averaged by site. Ordinations were performed using the metaMDS function in vegan (Oksanen et al. 2011) in R. Difference in composition among grassland types was tested using permutational MANOVA (Anderson 2001)

Table 1. Details on sites used in this study.

Site	Type	Area (ha)	% Native cover	Longitude	Latitude
3	Old field	16.5	32.2	−94.069376	40.690143
4	Old field	9.3	51.8	−94.064491	40.683107
6	Old field	15.6	35.7	−94.124854	40.611271
11	Old field	3.5	17.2	−94.120737	40.582275
9	Pasture	32.4	47.6	−94.136821	40.591692
10	Pasture	31.2	23.1	−94.124183	40.583996
12	Pasture	34.0	52.7	−94.140074	40.579071
13	Pasture	17.8	44.5	−94.175443	40.576261
1	Reconstruction	11.5	83.3	−94.093327	40.704849
2	Reconstruction	14.5	66.6	−94.074316	40.694498
5	Reconstruction	32.4	75.0	−94.107273	40.674720
16	Reconstruction	18.7	93.5	−94.114677	40.487575
7	Remnant	15.4	88.5	−94.135568	40.601074
8	Remnant	9.0	96.7	−94.140919	40.592168
14	Remnant	40.0	95.4	−94.130453	40.527235
15	Remnant	21.8	98.7	−94.143039	40.519640

Notes: Sites are numbered based on location from north to south (1–16) Percent native cover was estimated for each transect from 10 1 × 0.5 m quadrats along each transect and averaged by site. Latitude and Longitude are represented in decimal degrees.

with the adonis function in vegan in R.

We calculated the change in species composition from round to round for each transect using the vegdist function in vegan in R, employing Bray-Curtis Dissimilarity as the dissimilarity measure. The coefficient of variation (CV = σ/μ) was calculated across all round to round comparisons throughout the season for each transect. Differences in the coefficient of variation among grassland types was tested using a mixed effects-model using the lme function in the nlme package in R with site as a random variable. Finally, figures in this manuscript were constructed using the ggplot2 package (Wickham 2009) in R.

Results

We counted 296,256 inflorescences from a total of 142 species across the 12 sampling rounds; 113 of the species were native and 29 were classified as exotic. Total abundance of inflorescences did not differ among grassland types ($F = 0.4$, $p = 0.78$; Fig. 2A), but richness did ($F = 6.1$, $p = 0.0005$; Fig. 2B). Remnants and reconstructions supported the highest species richness of flowering plants and differed from the richness of old fields ($p < 0.001$ and $p = 0.028$; respectively), using Tukey's multiple comparison test. Pastures exhibited a marginally statistically significantly greater richness as compared to old fields ($p = 0.051$), using Tukey's multiple comparison test. Native species richness differed among all Tukey's multiple comparison tests ($p < 0.05$) except for the contrast between reconstructions and pastures ($p = 0.772$). Specifically, native richness was greatest in remnant prairies and lowest in old fields, while native richness in reconstructions and pastures was intermediate between the two.

Within individual sampling rounds, grassland types showed few differences in abundance and richness of floral resources (Fig. 3A, B). In terms of abundance, there were no statistically significant differences among grassland types within individual rounds after Bonferroni correction for multiple tests ($p < 0.05/72 = p < 6.9 \times 10^{-4}$). In terms of richness, there were several differences among grassland types within individual rounds following Bonferroni correction ($p < 6.9 \times 10^{-4}$) as follows: richness was greater in pastures than in old fields in rounds 3 and 4 ($p = 4.5 \times 10^{-5}$ and $p = 8.6 \times 10^{-6}$, respectively), in round 11 richness was higher in remnants than pastures and old fields ($p = 3.0 \times 10^{-4}$ and $p = 5.7 \times 10^{-5}$, respectively). In round 4, pastures had marginally significantly greater richness than reconstructions ($p = 7.1 \times 10^{-4}$).

NMDS ordination indicated that composition showed similar trajectories among all four grassland types over the course of the season (k = 2, stress = 9.74%; Fig. 4A). Sites were least similar at the beginning of the season and became more similar over time. Reconstructed prairies were the most dissimilar from remnant prairies during the first three sampling rounds (3

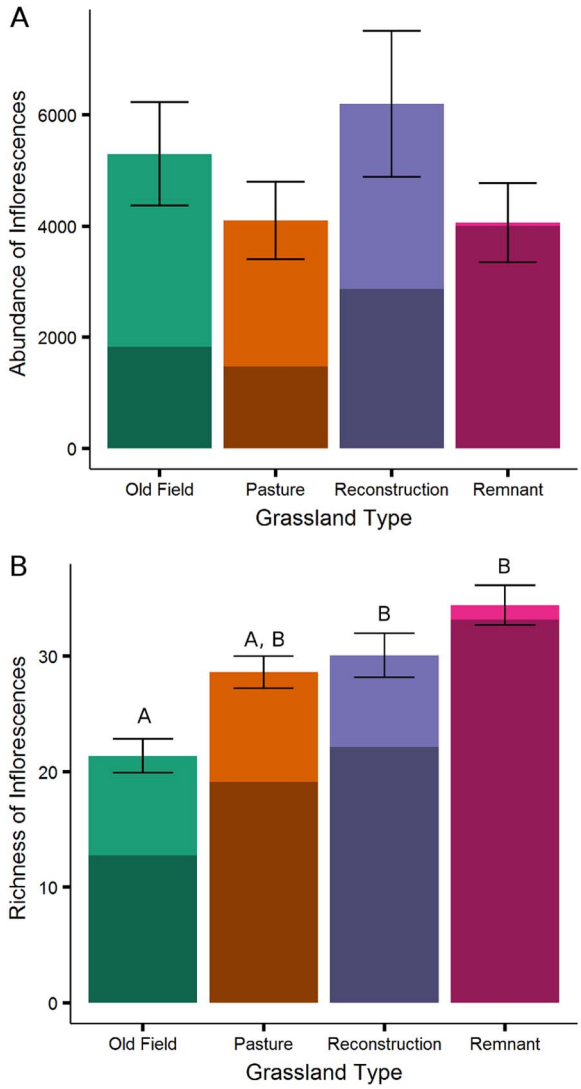

Fig. 2. The average seasonal total abundance (A) and seasonal total richness (B) of inflorescences among grassland types with four transects within each site. Seasonal total of abundance (A) did not differ among grassland types. Statistically significant differences in seasonal total of richness of inflorescences are indicated by different letters. Shaded portions of each bar represent the proportion of native inflorescences. Error bars depict standard error of the mean.

May–1 June), and then shifted to being the most similar to remnant prairies beginning in round four (14 June). When we compared composition based on seasonal total inflorescences there were differences among grassland types ($F = 2.60$, $p = 0.001$), with remnant prairies being the least similar to the other three grassland types (k = 3, stress = 7.43%; Fig. 4B).

All grassland types showed similar change in composition from round to round over the course of the study (Fig. 5). Only the fifth comparison between rounds showed differences among grassland types after Bonferroni correction ($p < 0.05/66 = p < 7.6 \times 10^{-4}$). Specifically, Bray-Curtis dissimilarity between rounds was greater in remnants than old fields and pastures ($p = 3.7 \times 10^{-5}$ and $p = 1.8 \times 10^{-4}$, respectively). Grassland types differed in terms of variability indicated by the coefficient of variation in change in composition from round to round throughout the season ($F = 4.90$, $p = 0.02$; Fig. 6), with remnant prairies having less variability than pastures after Tukey's multiple comparison test ($p = 0.02$).

Discussion

Our results have demonstrated differences in the availability of floral resources among grassland types of the Upper Midwest, and these differences could have implications for pollinators. The importance of a diverse diet has been verified for some pollinators. For example, Alaux et al. (2010) found that honeybees fed diets of pollen from multiple sources had greater immunocompetence than honeybees who fed on pollen from a single flower source. Similarly, Tasei and Aupinel (2008) demonstrated that bumblebee larvae were heavier when fed a diet from multiple pollen sources than when fed pollen with greater protein content that came from a single flower source. The importance of diverse diet is even evident in foraging data. Bumblebees have been shown to travel farther to forage in species-diverse floral patches even when less diverse but florally dense patches are available at shorter distances from the nest (Jha and Kremen 2013).

Species richness

Consistent with our prediction of cross-season total species richness, old fields had the lowest richness and differed from remnant and reconstructed prairies. Kwaiser and Hendrix (2008) found similar results wherein the abundance, richness, and diversity of floral resources was lower in old fields compared to remnant prairies.

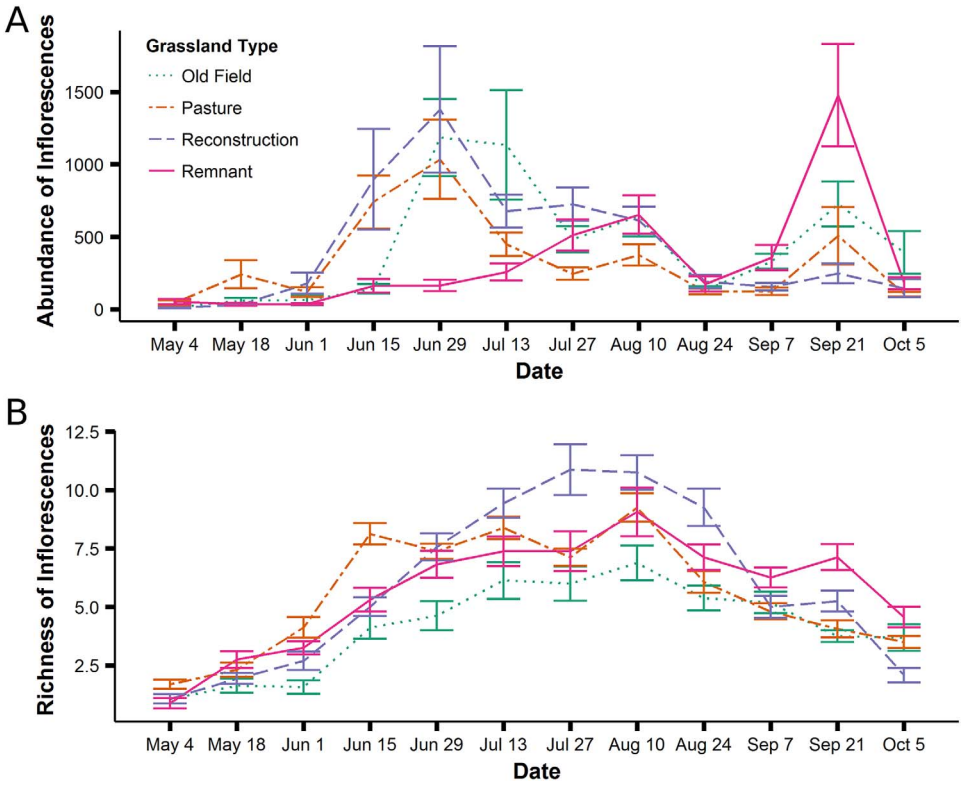

Fig. 3. Seasonal changes in the average abundance (A) and richness (B) of inflorescences for each grassland type, with four transects within each site. Each round was sampled at a two week interval beginning on a Friday or Saturday and ending on a Saturday or Sunday beginning on 3 May and ending on 5 October in 2013. Dates listed on this graph are the Saturday date of each sampling round. There were no differences with comparison among grassland types within a single round in terms of the abundance of inflorescences. Richness was statistically significantly greater in pastures than in old fields in rounds 3 and 4, in round 11 richness was statistically significantly higher in remnants than pastures and old fields. See results for specific details on specific statistics. Error bars depict standard error of the mean.

Farhat et al. (2014) did not find differences in richness of flowers between old fields and reconstructed prairies, but did find differences in terms of floral quality index. The differences in richness of floral resources among grassland types found in this study concur with other research demonstrating differences in terms of biodiversity, productivity, phenology, ecosystem services etc. when conducting comparisons between remnant grasslands and grasslands that consist of a mix of native and exotic species such as our old fields and conservation grazed cattle pastures (Wilsey et al. 2009, 2011, Isbell and Wilsey 2011, Martin et al. 2014).

When comparing richness of native forb species, all grassland types differed from each other except for reconstructed prairies and pastures. The proportion of native flower species was particularly high in the remnants and comparatively lower in the other three grassland types. The degree to which exotic plant species may benefit pollinators is currently unclear (Palladini and Maron 2014). Exotic nectar and pollen sources are thought to be potentially valuable supplemental resources for native pollinators (Bjerknes et al. 2007, Tepedino et al. 2008). However, this pattern may only apply to generalists; pollinators that specialize on native plants may be negatively affected by the presence of exotic plant species (Stout and Morales 2009). We included both native and exotic species in our analyses because we expected the exotic species

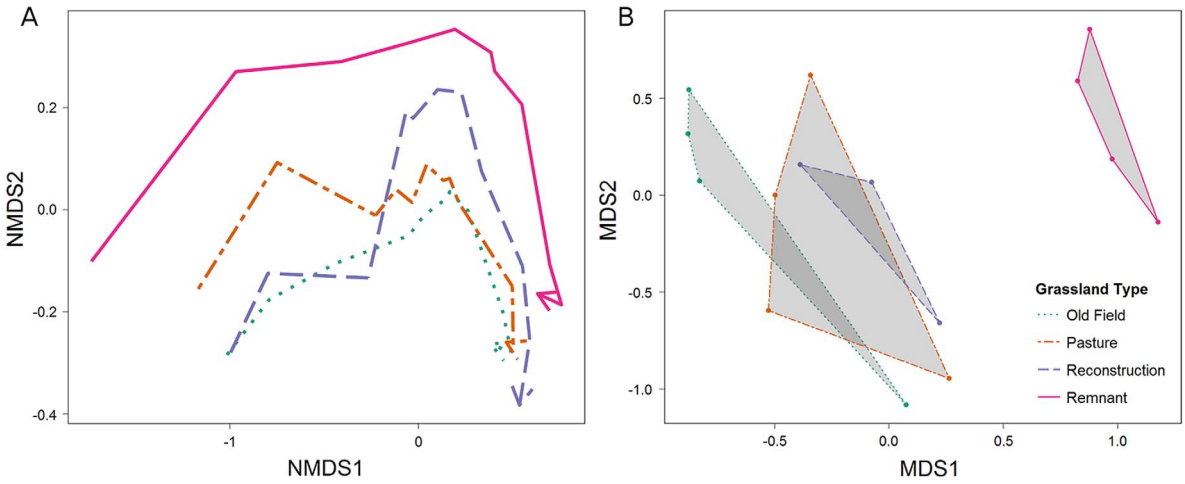

Fig. 4. Ordination diagrams showing seasonal changes in composition (A) and differences among grassland types in total composition (B). Lines in diagram A follow the centroids (average) of each of the four sites within a treatment through each round across the season. See methods and results for details.

to represent adequate resources for many of our pollinator species (Tepedino et al. 2008) and because interactions between pollinators and plants tend to be fairly generalized (Burkle and Alarcón 2011).

Despite our predictions, the four different grassland types that we examined showed surprising similarity in their seasonal succession of both abundance and richness of inflorescences. At no point in the growing season did the abundance of inflorescences differ among grassland types but it became markedly greater for all grassland types except remnant prairies from rounds four through six (14 June to ~15 July). This pattern was primarily driven by flowering of *Erigeron* spp., *Lotus corniculatus*, *Melilotus officinalis*, and *Trifolium spp*. With the exception of *Erigeron* spp., these are species commonly introduced in agricultural landscapes (Stubbendieck et al. 1994), and were found less frequently

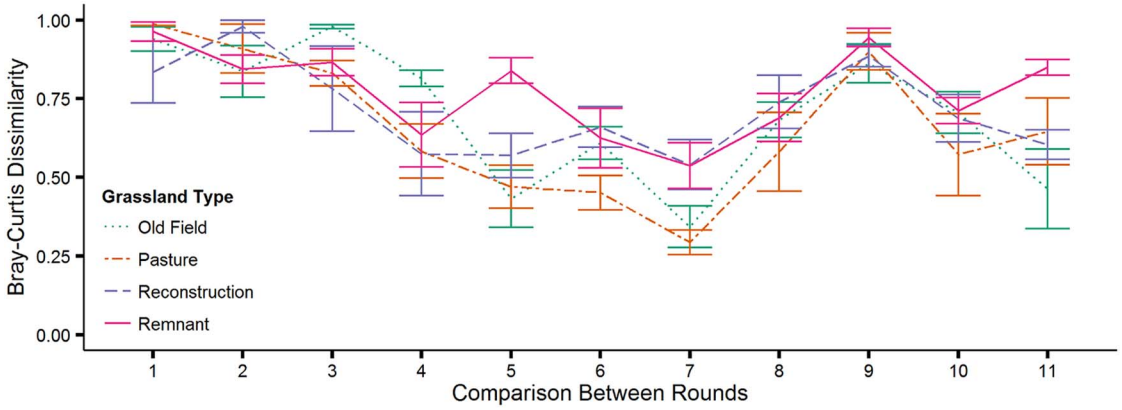

Fig. 5. Seasonal changes in turnover in species composition from one round to the next for each of the grassland types. Remnants differed statistically significantly from pastures and fallow fields in round 5. Difference in composition is measured using Bray-Curtis dissimilarity where 1.0 indicates no species were shared and 0.0 indicates no difference in composition (i.e., both identical species and abundances for each species). Error bars depict standard error of the mean.

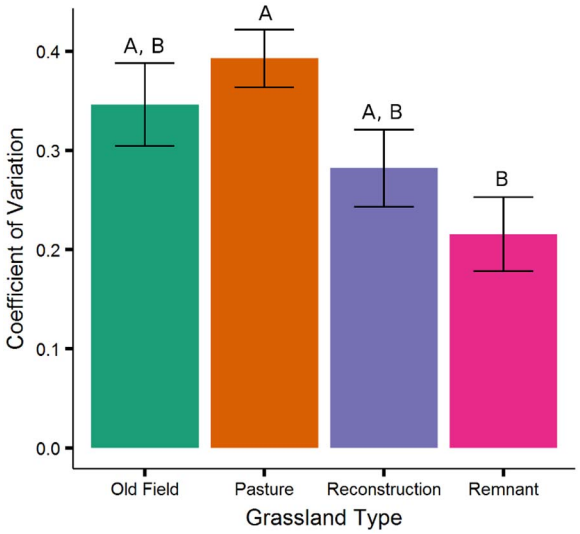

Fig. 6. Coefficient of variation (CV = σ/μ) in turnover in species composition across the season for each of the grassland types. Statistically significant difference in the coefficient of variation among grasslands types are indicated by letters above each bar. Error bars depict standard error of the mean.

in remnant prairies. Another observation of note is that abundance of inflorescences was highest in round two (18 May) in cattle pastures and highest in round 11 (21 September) in remnant prairies. The early spring and early fall periods are important foraging times for both honey bee and bumblebee colonies. Based upon the abundance of inflorescences, pollinators may benefit from nearby conservation grazed cattle pastures in the spring and remnant prairies in the fall.

All four of the grassland types showed a general pattern of highest richness in the mid-season, which has been observed in other regions of the tallgrass prairie (Anderson and Adams 1981, Craine et al. 2012). Reconstructed prairies exhibited a distinctive mid-season peak in richness of inflorescences, which was more pronounced compared to other grassland types. This pattern coincides with our prediction that reconstructed prairies would show a strong midseason peak with lower richness early and late in the season because of the observation that prairie reconstruction plantings favor species that flower mid-summer. Species most frequently encountered in reconstructed prairies in this study included *Dalea purpurea*, *Heliopsis helianthoides*, *Hypericum ascyron*, *Liatris pycnostachya*, *Melilotus officinalis*, *Monarda fistulosa*, *Oligoneuron rigidum*, *Penstemon digitalis*, *Potentilla arguta*, *Silphium perfoliatum*, and *Trifolium hybridum*, most of which reached peak bloom in the middle of the season between the fifth and ninth sampling rounds (~29 June to ~24 August). Reconstructed prairie plantings may be an important resource for pollinators foraging in the middle of the season and their integration within agricultural landscapes is likely to benefit pollinators. Alternatively, highly attractive floral displays may act as a sink (Thomas and Kunin 1999) if adequate resources for larval stages are absent (e.g., nesting sites for bees or larval host plants for butterflies).

Community composition

With respect to the overall community composition of flowering plants across the season, remnant prairies were the most dissimilar to the other grassland types, as we had predicted. In our ordination illustrating seasonal change in composition, we see several patterns that were not testable, but are validated in the context of what is commonly known about our four grassland types. Grassland types showed the greatest dissimilarity in ordination space early in the season. Common early blooming exotic species included *Barbarea vulgaris* and *Taraxacum officinale*, and these species were encountered in all grassland types except for remnant prairies. Early blooming native tallgrass prairie species in this study included *Antennaria neglecta*, *Comandra umbellata*, *Fragaria* spp., *Oxalis violacea*, *Pedicularis canadensis*, *Sisyrinchium campestre*, *Viola pedatifida*, and *Viola sororia*. None of these species occurred in reconstructed prairies or old fields with the exception of *V. pedatifida* that was found in reconstructed prairies. This highlights why reconstructions and old fields were most dissimilar from remnant prairies at the beginning of the season.

Reconstructed prairies became more similar to remnant prairies beginning in round four (~15 June), and remained that way for 14 weeks and then became less similar in mid-September onwards (the last two rounds). This pattern could indicate that (1) previous disturbance, perhaps early in the establishment phase, may have excluded early and late blooming species,

(2) establishment of prairie species in reconstructions favors native species that flower in the middle of the season, or (3) that seed mixes at these sites were deficient in early and late flowering native species. The inability of reconstructed prairies to mimic the diversity of remnant prairies has been previously recognized (Polley et al. 2005). Our results demonstrate that greater attention to early and late blooming species establishment and persistence in reconstructed prairies is needed in order to better mimic floral resource composition of remnant prairies throughout the entire growing season.

The cattle pastures used in this study are believed to have experienced minimal disturbance in the past aside from heavy cattle grazing and interseeding of exotic forage species. Thus, they retain some remnant flora and this may explain why they were more similar to remnant prairies at the beginning of the season. For early flowering native species, *Comandra umbellata*, *Oxalis violacea*, and *Pedicularis canadensis* were only encountered in remnant prairies, *Antennaria neglecta*, *Fragaria* spp., and *Viola pedatifida* were found in remnants and pastures, while *Sisyrinchium campestre* and *Viola sororia* were more common in pastures than they were in remnant prairies.

The convergence among all grassland types later in the season is likely explained by the tendency for later flowering species to be common species across all four grassland types. For example, species that were common later in the season tend to occur in a range of habitats from high-quality to degraded. The most abundant late season species in this study (i.e., making up 94% percent of total abundance of inflorescences of the 35 blooming species encountered in the last two rounds) were *Solidago canadensis*, *Symphyotrichum ericoides*, *Symphyotrichum lanceolatum*, and *Symphyotrichum oolentangiense*, most of which have low coefficient of conservatism values (0, 3, 4, and 7 respectively; Drobney 2014).

Composition turnover was not consistently lower in conservation grazed cattle pastures as we predicted, but the variability in composition turnover was greater in cattle pastures than in remnant prairies. Although the richness of inflorescences between remnant prairies and cattle pastures was equivalent throughout much of the season, the resources that were available to pollinators did not change from round to round as consistently in cattle pastures as they did in remnant prairies. The lowest period of turnover in pastures occurred during comparisons five through seven. It is possible that the variability in turnover in pastures could be reduced by the establishment of native species. Based on our data, potential candidate species that could increase diversity over this time period include *Chamaecrista fasciculata*, *Dalea purpurea*, *Desmodium canadense*, *Heliopsis helianthoides*, *Monarda fistulosa*, *Parthenium integrifolium*, *Potentilla arguta*, *Ratibida pinnata*, and *Rudbeckia hirta*. However, further research is required to investigate the ability of these species to persist in a managed grazing system.

Rotenberry (1990) found a similar variability in turnover of inflorescence composition in an old field dominated by exotic species in northern Michigan, USA. In our study, old fields had the second highest (but not statistically significantly higher) variability in composition turnover. Recent studies have demonstrated the importance of floral resource diversity for pollinator health of honey bees and bumble bees (Tasei and Aupinel 2008, Alaux et al. 2010, Jha and Kremen 2013). Thus, it seems reasonable to assume that periods of low turnover in floral resources (i.e., lower diversity over time) could be problematic for long-lived pollinators that require a diverse diet. However, we are not aware of any study that specifically investigates the effect of floral resource diversity over time on the health of long lived pollinators such as honey bees or bumble bees.

Future research

While the importance of abundant and diverse sources of floral resources for pollinators has been demonstrated in multiple studies (Tasei and Aupinel 2008, Alaux et al. 2010, Jha and Kremen 2013), the degree to which the differences among grassland types found in this study translate to ecologically significant influences on different pollinator taxa is beyond the scope of this paper. Likewise, differences among grassland types that did not fall below the stringent significance thresholds could still have important ecological implications. Understanding how pollinator communities differ among grassland types is an

essential next step and necessary to demonstrate whether differences are truly ecologically significant. This study provides a valuable baseline for studies in the tallgrass prairie ecoregion to investigate the responses of various pollinator taxa to differences in floral resource availability among grassland types.

An important next step in understanding seasonal succession patterns in floral resource availability would be to quantify interannual variation among grassland types. It would also be valuable to investigate the degree to which pollinators switch between grassland types throughout the season in response to floral resource availability. For example, the abundance of floral resources was very high in non-remnants from rounds four through six (~15 June to ~13 July), and as such, these sites may have attracted pollinators from remnants.

Finally, future research should consider how short or infrequent sampling periods could bias scientific interpretation of the availability of floral resources and pollinator responses. For example, our ability to detect statistically significant differences among grassland types within some rounds but not others (even with very low significance threshold used to account for multiple tests) illustrates the importance of considering how sampling time within the season could influence interpretation of floral resource availability.

Implications for conservation and management

(1) *Old fields* were the grassland type most consistently different from remnant prairies. Given these findings, our results indicate that targeted efforts to enhance floral diversity on old fields could accomplish the largest potential change in resources for pollinators.

(2) *Conservation grazed cattle pastures* showed the greatest variability in composition turnover throughout the growing season. Interseeding native plant species that are tolerant of grazing and bloom during periods of low turnover could improve pollinator resources in conservation grazed cattle pastures.

(3) *Reconstructed prairies* showed the strongest midseason peak in richness of inflorescences, and differed in composition from remnants at the beginning and end of the season. Greater efforts to establish early and late blooming species to better mimic remnant composition would enhance pollinator resources at these sites.

(4) *Remnant prairies* showed the largest difference in composition compared to the other three habitat types and supported the greatest abundance and richness of flowering native plants. The preservation of remnants will be essential for maintaining native pollinator diversity, particularly for insect and plant species with specialized plant-pollinator interactions.

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Supplemental Material

Ecological Archives

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REVIEW / SYNTHÈSE

The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined?[1]

Robert J. Fletcher, Jr., Leslie Ries, James Battin, and Anna D. Chalfoun

Abstract: Over the past few decades, much research has focussed on the effects of habitat area (i.e., patch size) and edges in fragmented landscapes. We review and synthesize the literature on area and edge effects to identify whether the ecological processes influenced by patch size and edge are distinct, to summarize evidence for the relative effect of each, and to discuss how estimating their independent effects may be accomplished in field studies. Area and edge directly influence ecological processes in distinct ways, yet indirect effects can be similar, making it difficult to isolate the effects of area and edge in nature. Many studies investigating both area and edge have been confounded in their design and (or) analysis (i.e., studies did not control for one potential effect while testing for the other). Nonconfounded studies have more frequently shown support for edge effects, and comparisons between nonconfounded and confounded studies suggest that some observed area effects could be explained by edge effects. We argue that by focussing on the fundamental processes directly influenced by area and edge, and by developing more rigorous study designs and analyses that isolate their relative influence, greater insight can be gained in future investigations on habitat loss and fragmentation.

Résumé : Au cours des quelques dernières décennies, beaucoup de travaux se sont intéressés aux effets de la surface de l'habitat (c'est-à-dire la taille des taches) et des lisières dans les paysages fragmentés. Nous passons en revue et résumons la littérature sur les effets de la surface et des lisières afin de déterminer si les processus écologiques influencés par la surface et les lisières sont différents, de résumer l'information sur les effets relatifs de chacune de ces variables et d'examiner comment estimer leurs effets respectifs dans des études de terrain. La surface et les lisières affectent directement les processus écologiques de façon distincte, mais leurs effets indirects peuvent être semblables, ce qui rend la distinction entre les effets de la surface et ceux des lisières difficile en nature. Plusieurs études qui considèrent la surface et les lisières confondent les deux variables à cause de leurs plans d'expérience et (ou) d'analyse (c'est-à-dire elles ne tiennent pas compte d'un effet potentiel en testant l'autre). Plus fréquemment, les études qui ne confondent pas les deux variables ont découvert des indications de l'existence d'un effet des lisières; de plus, une comparaison d'études avec ou sans variables confondues indique qu'une partie des effets attribués à la surface peut s'expliquer par les effets des lisières. Nous croyons qu'en se concentrant sur les processus fondamentaux influencés directement par la surface et les lisières et en mettant au point des plans d'expérience et d'analyse plus rigoureux pour isoler les effets relatifs de chacune des deux variables, il sera possible d'obtenir de meilleures perspectives dans les recherches futures sur la perte et la fragmentation des habitats.

[Traduit par la Rédaction]

Introduction

Landscapes are composed of a patchwork of habitats that vary in size, shape, and location. Ongoing habitat loss continues to influence landscape structure, with habitat loss generally leading to increased fragmentation of habitats (or the breaking apart of habitat, independent of loss; Wiens 1995; Fahrig 2003), whereby patches decline in size, increase in isolation, and increase in the proportion of edge

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[1]This review is one of a series dealing with some aspects of the impact of habitat fragmentation on animals and plants. This series is one of several virtual symposia focussing on ecological topics that will be published in the Journal from time to time.
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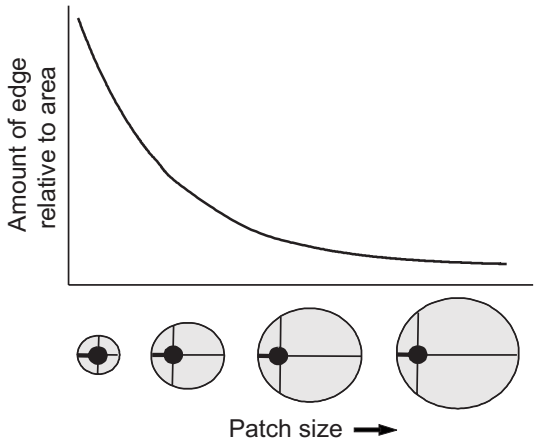
habitat. Because habitat loss is often implicated as the most important threat to biodiversity (e.g., Wilcove et al. 1998), understanding how habitat loss and fragmentation influence ecological patterns and processes has been (Gates and Gysel 1978; Ambuel and Temple 1983), and continues to be (Tscharntke and Brandl 2004; Ewers and Didham 2006), a central focus of landscape ecology, population and community ecology, and conservation biology.

Both habitat area and isolation have long been considered important in affecting ecological patterns and processes. For instance, the equilibrium theory of island biogeography (ETIB hereinafter) and metapopulation theory incorporate area and isolation to explain variation in community structure and population dynamics, respectively (MacArthur and Wilson 1967; Levins 1969; Hanski 1998). These theories have also been applied to understand habitat loss and fragmentation, but with limited success (Doak and Mills 1994; Wiens 1995; Gascon and Lovejoy 1998; Laurance et al. 2002). One explanation for this limited success is that the boundaries of habitat fragments — habitat edges — can also profoundly influence ecological patterns and processes (Gascon and Lovejoy 1998). In fact, a survey of recent experiments on habitat fragmentation suggested that habitat edges are the primary drivers for the influence of fragmentation (Harrison and Bruna 1999).

Over the past three decades, a great deal of research has focussed on the influence of habitat edges and area on a wide diversity of patterns and processes in fragmented landscapes. Much of this research has been driven by concern for recent population declines of many species (e.g., Herkert 1994), improved technology that allows rapid assessment at broad spatial scales (e.g., Alencar et al. 2004), and an increasing awareness that space can have novel effects on a variety of ecological and evolutionary processes (e.g., Kareiva 1990). Yet, attempts to provide conceptual and predictive frameworks to guide our understanding of the unique roles of habitat area and edge have been rare (but see Ries and Sisk 2004).

While both habitat area and edge may influence individuals, populations, and communities, understanding the relative role of these landscape characteristics is crucial for implementing sound conservation strategies. Because habitat area and edge reflect different aspects of landscape structure — landscape composition and configuration, respectively (McGarigal and Marks 1995) — the importance of each suggests different foci for conservation efforts. Furthermore, when habitat edges are implicated in the effects of fragmentation, the type of edge often influences observed outcomes (Sisk et al. 1997; Chalfoun et al. 2002*a*; Fletcher and Koford 2003; López-Barrera et al. 2006), suggesting that managers and conservationists may need to focus on specific attributes that surround remaining fragments. Habitat area and edge in landscapes nonetheless tend to covary in their amount (Fig. 1), and many studies have not been able to isolate the unique contributions of each element (Parker et al. 2005). Another complication is that effects from habitat edges may explain observed area effects (Bowers et al. 1996; Laurance et al. 1998; Fletcher 2005), making it difficult to interpret if purported area effects are actually a manifestation of edge effects. These problems are exacerbated when considering the cumulative influence of multiple edges within fragments (Fig. 1), as opposed to only the influence of the nearest edge (Malcolm 1994; Fletcher 2005).

Fig. 1. The interplay of patch size and edge. As patch size decreases, the relative amount of edge increases. In addition, the influence of multiple (all surrounding) edges is exacerbated in smaller patches. This pattern is shown by the point in each patch of increasing size, which all have the same nearest distance to edge (marked by the thick lines to the left of the solid circles). However, as patch size increases, the cumulative distance to all edges also necessarily increases (illustrated in the four cardinal directions), and typically does so in an exponential manner.



Our objective is to examine the effects of both area and edge to better understand their unique contributions to habitat fragmentation. We first synthesize separate conceptual frameworks for the mechanisms that underlie area and edge effects. We then examine the literature where both edge and area effects were measured within the same investigation to determine their relative contribution to fragmentation dynamics. We conclude by discussing how future field studies should be designed to limit the potential confounding issues that arise when investigating the role of area and edge in fragmented landscapes. For the purposes of this article, "patch size effects" are changes in ecological responses (per unit area) as a function of patch area per se, and thus independent of other potential causes, such as those arising from changes in the relative amount of edge. Alternatively, we use "area effects" as a broader term that describes changes in ecological responses with habitat area, which may or may not be independent of other potential causes (a definition implicitly used in the literature), such that patch size effects are a subset of area effects. We do not include studies that examine total habitat area within a landscape because issues of scale and landscape context make inferences on the effective area available to organisms difficult to interpret. "Edge effects" are changes in ecological responses that vary with distance from edge (Ries et al. 2004). Interpreting the unique roles of patch size and edge will improve our understanding of habitat fragmentation and help to refine conservation strategies aimed at mitigating the effects of habitat loss and fragmentation.

Conceptual frameworks for edge and area effects

Investigations on habitat area and edge have largely been

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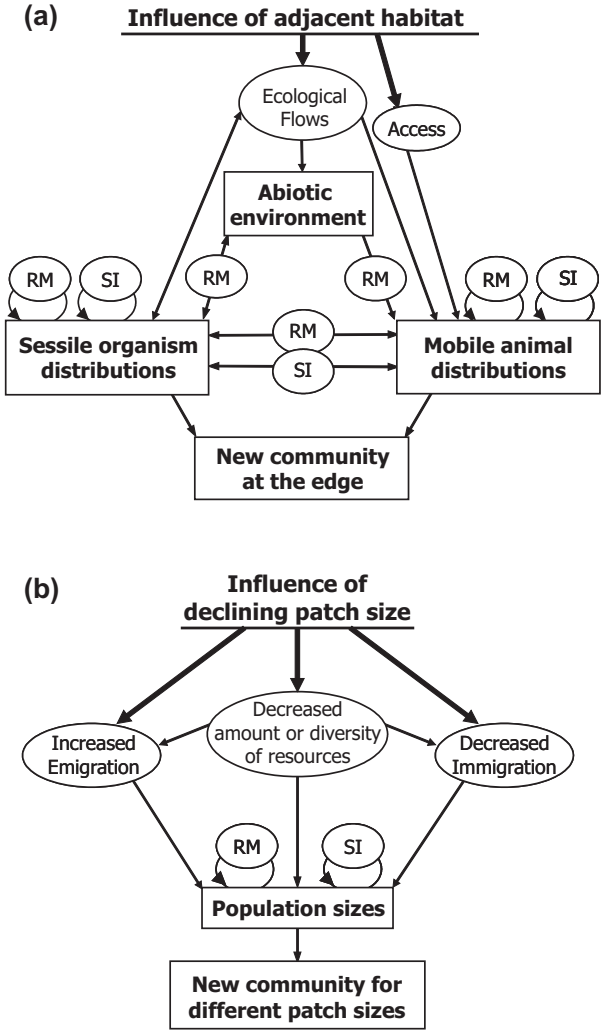
conducted separately, with relatively few attempts to explicitly compare the influence of both landscape elements. Investigations on habitat area have centered on either the ETIB or metapopulation theory and determining their applicability in fragmented landscapes (e.g., Hanski 1998; Ricketts 2001; Brotons et al. 2003). Researchers have proposed several mechanisms for the influence of habitat area (MacArthur and Wilson 1967; Root 1973; Gilpin and Diamond 1976; Ambuel and Temple 1983; Matter 1997; Fletcher 2006), yet there is much overlap in the description and interpretation of these mechanisms (see Brotons et al. 2003), with no current framework that describes and links fundamental mechanisms for area effects. Similarly, a large literature has provided a suite of potential mechanisms underlying edge effects (Wiens et al. 1985; Murcia 1995; McCollin 1998; Fagan et al. 1999; Cadenasso et al. 2003). Ries et al. (2004) recently synthesized the proposed mechanisms for edge effects into a unified conceptual framework, focussing on how habitat edges influence the distribution and abundance of organisms. Below, we briefly review their framework and apply a similar approach to understand how area influences ecological patterns and processes, highlighting empirical examples that find evidence for such mechanisms.

Mechanisms of edge effects

Habitat edges fundamentally influence ecological processes in two direct ways: (1) by altering the flows of energy, materials, and (or) organisms and (2) by providing access to spatially separated resources (Ries et al. 2004). These two direct effects can lead to indirect effects through resource mapping and species interactions (Fig. 2*a*), all of which may lead to changes in populations and community structure near edges (Fagan et al. 1999; Ries et al. 2004). Resource mapping occurs when an organism's distribution reflects ("maps" onto) that of its resources (see Ries et al. 2004). Changes in species interactions include variation in predator–prey interactions (Ries and Fagan 2003), competition (Suarez et al. 1998), or facilitation (Jules and Rathcke 1999) near edges. These direct and indirect effects capture most dynamics that occur near edges (McCollin 1998; Fagan et al. 1999; Ries et al. 2004). Much of the observed variation in dynamics near edges can be explained by the edge type investigated, where the type of habitat surrounding fragments has the potential to influence each of the aforementioned mechanisms (Ries and Sisk 2004; Ries et al. 2004).

The flow of materials and organisms can be influenced by edges, where habitat boundaries can amplify, attenuate, or reflect flows into and out of adjacent patches (Strayer et al. 2003). In turn, variation in ecological flows can lead to abundance and (or) diversity gradients near edges, which can be influenced by edge contrast (Stamps et al. 1987), the surrounding matrix (Ricketts 2001; Chalfoun et al. 2002*a*), and species' life histories (Henle et al. 2004). Ecological flows are predicted to cause declines in abundance near edges within preferred habitat, but increases in abundance within the adjacent habitat caused by "spillover" (Ries and Sisk 2004). There are numerous examples of edges influencing ecological flows, including energy flows that impact microclimate (Chen et al. 1995), seed dispersal (Cadenasso

Fig. 2. Conceptual frameworks that identify different process-based pathways by which the distribution of organisms are influenced by habitat edge and patch size, where thick arrows denote direct effects of edge and patch size and arrows denote indirect effects. (*a*) Habitat edges directly influence the ecological flow or movement of materials, energy, and organisms, as well as directly providing access to spatially separated resources for mobile organisms. These issues indirectly influence resource mapping (RM) and species interactions (SI). (Modified from Ries et al. 2004, reproduced with permisson of Annu. Rev. Ecol. Evol. Syst., vol. 35, p. 496, © 2004 Annual Reviews.) (*b*) Declines in patch size from habitat loss and fragmentation directly result in a reduction of the amount and (or) diversity of available resources. Declining patch size also alters the likelihood of movement into and out of patches by dispersing individuals, with most theory assuming that declining patch size increases emigration and decreases immigration rates. Emigration and immigration can be directly influenced by changes in patch geometry within landscapes (e.g., the "target" effect) or indirectly through changes in resource concentration. These issues are predicted to generally decrease population size and increase local extinction risk of organisms, which have indirect effects on resource mapping and species interactions. Indirect effects of resource mapping and species interactions can be variable, however, leading to potentially complex effects on resulting population and community dynamics. See text for details.



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and Pickett 2001), and animal movement, with butterfly movement particularly well studied (Haddad 1999; Ries and Debinski 2001; Schultz and Crone 2001; Schtickzelle and Baguette 2003). A rigorous example highlighting the consequences of ecological flows comes from a recent experiment by Levey et al. (2005), who demonstrated that the effects of corridors on seed dispersal by birds could best be explained by edge effects: individuals encountering edges tended to reflect back into the focal patch, which in turn led to extensive use of corridors.

Mobile organisms, as opposed to sessile ones (Fig. 2*a*), near edges may also gain access to resources from adjacent habitats (Rand et al. 2006). If organisms gain access to such spatially separated resources, an increase in the density of individuals is predicted near edges. In a classic example, aspen experienced the heaviest outbreaks of a leaf-mining insect (*Phyllonorycter salicifoliella* (Chambers, 1875)) near stands of coniferous trees, which *P. salicifoliella* used as overwintering sites (Martin 1956).

Changes in ecological flows often result in distinct resource gradients near edges, which influence the distribution of the plants and animals that map onto changes in those resources. Such resource mapping can occur via plants and animals mapping onto gradients in abiotic or plant resources, or via animals mapping onto other animal resources (Ries et al. 2004). For example, foraging behaviors of white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) in forest fragments of Ohio suggested that increased food availability may explain elevated mouse densities near edges (Wilder and Meikle 2005). While resource mapping can result in either increases or decreases in abundance and diversity, knowledge of relative habitat use can allow investigators to predict responses to edges (Ries and Sisk 2004; Ries et al. 2004).

Finally, much theoretical and empirical research has centered on the indirect effect of habitat edges on species interactions (Fagan et al. 1999; McGeoch and Gaston 2000; Chalfoun et al. 2002*b*). For instance, many investigations have estimated whether predation on bird nests increases near edges, with highly variable results, yet much of this variability can be explained by edge type, knowledge of specific predator behavior (which is often not measured), and landscape context (Paton 1994; Hartley and Hunter 1998; Lahti 2001; Chalfoun et al. 2002*a*, 2002*b*; Stephens et al. 2004). Fewer empirical examples exist for changes in other species interactions near edges. In a rare example, Suarez et al. (1998) reported that Argentine ants (*Linepithema humile* (Mayr, 1868)) found predominantly near edges appear to outcompete the local, native ant species.

Mechanisms of area effects

To address mechanisms of area effects, we distinguish between mechanisms that generate patch size effects, as defined above, and other mechanisms that can lead to changes with area that do not occur from patch size effects. Furthermore, we differentiate between two alternatives when focussing on measures of population size and density: (1) population size changes with declining patch size, but population density remains constant, and (2) population density changes with patch size. The ETIB focussed on changes in species richness with island area based on variation in colonization and extinction rates (MacArthur and Wilson 1967); an implicit assumption of this theory is that population density remains constant with area (Andren 1994; Connor et al. 2000; Brotons et al. 2003). Yet if changes in density occur (Bowers and Matter 1997; Bender et al. 1998; Connor et al. 2000), populations and communities may be strongly influenced by effects of habitat loss and fragmentation. We first outline mechanisms that generate patch size effects (Fig. 2*b*), focussing on how patch size influences population size, density, and community structure, and subsequently note two primary factors that can lead to area effects which are not patch size effects.

Declines in patch size with habitat loss and fragmentation fundamentally influence the abundance of organisms in two direct ways. First, as patches decrease in size, declines in the amount or diversity of resources, or both, influence population sizes of plants and animals by altering carrying capacities. Second, variation in patch size also influences the extent of emigration and (or) immigration by dispersers (Root 1973; Gilpin and Diamond 1976; Risch 1981; Lomolino 1990). Together, these direct effects can further lead to indirect changes in species interactions and resource mapping, leading to changes in community structure (Fig. 2*b*).

As patch size declines, the most obvious effect is a decline in the amount and (or) diversity of resources available to organisms, yet this phenomenon can have potentially novel, cascading effects through indirect pathways (Fig. 2*b*). Indeed, when patch size declines to very small sizes, lack of resources or insufficient space may cause patches to fall below the minimum area requirements of individuals (e.g., territory size; Stratford and Stouffer 1999). The resource concentration hypothesis (Root 1973) states that smaller areas contain a lower concentration or diversity of resources (Fig. 2*b*), resulting in lower densities of individuals (see also Ambuel and Temple 1983). Lower concentrations of resources can reduce density through reduced local recruitment based on declining habitat quality (Risch 1981; Matter 1997). MacArthur and Wilson (1967) also highlighted that changes in habitat heterogeneity with declining area could lead to declines in species richness. Thus, the ETIB and the resource concentration hypothesis predict that declining resources should have a negative impact on population size and (or) density, which subsequently increases extinction probability (Didham et al. 1998*a*, 1998*b*), alters species distributions, and changes community structure. Indirect effects of variation in resource mapping can further influence populations and communities when declining patch size differentially affects some resources more than others (Fig. 2*b*).

Immigration and emigration rates are influenced by several factors, such as edge type (Ries and Debinski 2001), population density (Matthysen 2005), and habitat quality (Pulliam 1988). Nonetheless, declining patch size is generally thought to directly decrease immigration rates because individuals moving through a landscape are less likely to encounter small patches (the "target" effect; Gilpin and Diamond 1976; Lomolino 1990), thereby reducing population size and density (Fig. 2*b*). Bowman et al. (2002) recently reviewed general heuristic arguments regarding immigration and concluded, however, that while immigration may often increase with patch area, leading to larger population size,

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many immigration behaviors should actually contribute to a decline in density with increasing patch size. This relationship may occur because immigration rates per unit area are likely to decline owing to the negative exponential nature of patch circumference per unit area with increasing patch size (see also Hamback and Englund 2005). Conversely, individuals moving within smaller patches are more likely to encounter boundaries than those moving in larger patches (Stamps et al. 1987), thus consistently increasing emigration rates out of smaller patches (Bowman et al. 2002). For example, Cronin (2003*a*) found that a planthopper (*Prokelisia crocea* (Van Duzee, 1879)) exhibited higher emigration rates in small patches than in larger patches. Such variation in emigration rates is predicted to cause lower densities and community diversity in small patches (Fig. 2*b*).

Both emigration and immigration can also be indirectly influenced by patch size through changes in resource concentration (Fig. 2*b*; Root 1973), where higher concentrations of resources in large patches are thought to decrease emigration rates and increase immigration rates. For instance, some social behaviors, such as conspecific attraction (i.e., the use of conspecifics as positive proximate stimuli for selecting locations of habitat), may cause an increase in immigration and a decrease in emigration in large patches, leading to patch size effects, and, albeit weak, edge effects on density (Fletcher 2006). However, such behaviors are better explained by patch size than edge, because increasing patch size increases the opportunity for the presence of social cues, which may be used as indirect measures of resource quality.

Species interactions can be indirectly influenced by declining patch size when disproportionate changes in one species' density or behavior alter its interactions with other species (e.g., Orrock and Fletcher 2005). Both the enemies hypothesis (Root 1973; Risch 1981) and the density compensation hypothesis (MacArthur et al. 1972) have been developed to explain how species interactions are altered with declining patch size (Fig. 4); however, each focusses on different types of interactions and makes different predictions for changes in population density. The enemies hypothesis states that predators are more abundant or more effective in smaller areas of habitat (Root 1973; Risch 1981; Askins et al. 1987), thereby altering species interactions. For example, predators may forage for relatively longer periods per unit area in smaller patches because the distance to other resources is often greater than that in larger patches (Stephens and Krebs 1986). We note, however, that the original logic for the enemies hypothesis (Root 1973; Risch 1981) is specific to insect predator – herbivore interactions in monocultures and polycultures and may not apply broadly across taxa in fragmented landscapes. Furthermore, some empirical evidence suggests that predator density can actually increase with patch size (Chapin et al. 1998; Pardini 2004). Conversely, the density compensation hypothesis predicts that declining species richness with reduced area (MacArthur and Wilson 1967) will cause densities to increase owing to a decrease in interspecific competition (MacArthur et al. 1972). Other types of interactions may also be affected, such that density may increase or decline based on the specifics of each interaction.

Although some studies in fragmented landscapes have attempted to test for changes in movement, resource mapping, and species interactions with patch size, surprisingly few have shown strong mechanistic support for observed area effects. Many of these investigations have attempted to understand why some bird species are area sensitive, or avoid small patches. A recent example from Japan (Kurosawa and Askins 2003) showed that many forest birds occurred at lower densities in smaller patches, and such patches also contained higher densities of predators, providing some support for the enemies hypothesis. Similarly, Herkert (1994) found that many grassland birds were sensitive to area, and that for some species, such as Henslow's Sparrow (*Ammodramus henslowii* (Audubon, 1829)) and Savannah Sparrow (*Passerculus sandwichensis* (J.F. Gmelin, 1789)), small fragments contained fewer potential resources per unit area (based on habitat structure). However, in both of these examples, and indeed in many investigations on area effects (Parker et al. 2005), investigators did not isolate whether observed area effects were patch size effects.

Finally, there are two main factors that can generate area effects, such that observed effects are not actual patch size effects. First, the proportion of edge tends to increase with declining patch size (Fig. 1). If a species responds to edges, these responses can result in changes in density (or other metrics) in patches of different sizes (Sisk et al. 1997; Fletcher 2005), and could be falsely attributed to a patch size effect. Therefore, to understand the unique roles of area and edge in fragmented landscapes, we need to not only control for edges when investigating effects of area but also to focus on the direct mechanisms responsible for edge and area effects. Second, as sampling increases, so does the likelihood of detecting an individual or a species, resulting in increases in the likelihood of occurrence or species richness with area sampled (Connor and McCoy 1979; Horn et al. 2000). This relationship has been termed the random sampling hypothesis and can explain some observed area effects (Haila et al. 1993; Andren 1994; Horn et al. 2000). Variation in sampling effort, however, should not cause changes in density or other measures that do not increase with sampling (e.g., fecundity).

Interplay of area effects, edge effects, and landscape context

These conceptual frameworks highlight the distinctiveness of direct effects of patch size and edge on ecological patterns and processes, yet both edge and patch size can have indirect effects on species interactions and resource mapping, such that observed effects can appear similar in nature. For instance, if species interactions change as a function of patch size (Fig. 2*b*), these interactions will also inevitably vary with distance to edge across patches (Fig. 1). Consequently, isolating whether species interactions vary from edge or patch size will often be difficult. On the other hand, the direct effects of edge and patch size are distinct (Figs. 2*a*, 2*b*), such that by testing for these potential effects, we can draw stronger inference regarding the unique roles of area and edge.

Edge and area effects also have the potential to interact. For example, Kiviniemi and Eriksson (2002) found that plant species richness in grasslands of Sweden increased near edges in small fragments but declined in large frag-

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ments. Our conceptual frameworks (Figs. 2*a*, 2*b*) suggest that edge effects from variation in ecological flows could potentially have synergistic effects on patch area influencing the amount of resources, but there is no explicit empirical evidence that isolates this potential synergism. Indeed, little clear evidence currently exists for area and edge effects interacting in fragmented landscapes (Nour et al. 1993; Matthews et al. 1999; Galetti et al. 2003; Lienert and Fischer 2003; Fletcher 2005; but for a recent example see Ewers et al. 2007).

There is ongoing interest in determining when, where, and how the surrounding landscape influences populations and communities within focal areas. Landscape context influences edge effects primarily through variation in matrix quality. Matrix quality can alter changes in the movement, or flow, of materials, energy, and organisms — effects that are fundamentally linked with variation in the permeability of habitat boundaries (e.g., Collinge and Palmer 2002). While there has been interest in understanding how landscape context can influence edge effects (Donovan et al. 1997; Tewksbury et al. 1998; Chalfoun et al. 2002*a*), an outstanding question is whether matrix quality effects are in reality simply effects of different edge types (Fletcher and Koford 2003; Ries and Sisk 2004), or vice versa. That is, are purported matrix effects driven primarily by variation in local edge effects caused by different edge types, or are edge type effects actually generated by large-scale differences in matrix quality? Answers to this question would be extremely valuable in interpreting whether large-scale fragmentation constrains local processes or whether local processes "scale up" to generate large-scale patterns.

Landscape context may also influence area effects in that distances between habitats can alter effective population sizes when individuals use more than one patch (Diffendorfer et al. 1995). However, there are no current predictions for matrix quality altering patch size effects, based on the fundamental processes patch size influences (Fig. 2*b*). While matrix quality may influence the movement of organisms, thereby altering immigration probabilities, the relative "target" effect of area should not vary, all else being equal. However, matrix quality can sometimes become more important than area in driving immigration rates, such that patch size may explain less variation in movement than characteristics of the matrix (Bender and Fahrig 2005). When the surrounding matrix provides novel resources used by some individuals, densities can increase with declining patch size (Dunning et al. 1992; Norton et al. 2000; Davies et al. 2001; Estades 2001), yet such density elevation is not driven by patch size effects. Instead, such effects are more directly related to edge effects allowing access to spatially separated resources (Didham et al. 1998*a*).

The relative role of area and edge: empirical evidence

To explore the relative roles of habitat area and edge, we reviewed studies that simultaneously tested for both effects in fragmented landscapes within an investigation. We focussed on three key questions. First, do investigators design studies that limit the potential confounding of area and edge when addressing these effects? Second, do studies more frequently find evidence for edge or area effects? Third, do investigators test for fundamental mechanisms responsible for patch size and edge effects? We also address whether results vary when comparing confounded and nonconfounded studies, and whether results vary depending on taxonomic group, the metric used, or habitat type.

Review methods

We first screened 231 articles gleaned from the *Web of Science*, using "patch size* AND edge* AND fragment*", "habitat area* AND edge* AND fragment*", "area effect* AND edge* AND fragment*", and "fragment size* AND edge*" as key words (accessed 14 March 2006). We also supplemented this list with other relevant articles. From these articles, 60 tested for both the effects of area and edge. For this review, we considered habitat area to include only issues of patch size and did not consider landscape-level analyses (e.g., Belisle et al. 2001; Fletcher and Koford 2002). For edge effects, we considered studies that estimated responses at the within-patch scale, using distance to edge, and at the patch scale, using measures of patch shape (e.g., perimeter to area ratios).

Our overarching goal was to determine if studies more commonly showed evidence for edge or area effects. As such, we focussed on within-study, pairwise comparisons that used similar methodologies to interpret the evidence for edge and area effects. Some investigations tested for both area and edge, but used different patches, different sampling units, or different species for each test (Dijak and Thompson 2000; Beier et al. 2002; Cronin 2003*b*); such studies were omitted. To limit biases from variation in sampling effort, we also only included studies with equal sample sizes for testing the effects of area and edge for a given response variable. We inferred sample size based on either the reported denominator degrees of freedom or on reported sampling units used for analyses. These criteria reduced the data set to 38 articles with 213 response variables measured. Our approach controlled for many issues that arise when summarizing effects across studies, as is often attempted in meta-analytic approaches (e.g., Bender et al. 1998; Connor et al. 2000). Yet we chose not to perform a formal meta-analysis for several reasons. First, we emphasize that our goal was not to estimate overall effect sizes, which would be highly variable across studies depending on the taxa and metric investigated, but instead to identify the relative support for area or edge effects within investigations. Second, formal meta-analyses primarily attempt to control for variation in sample size across studies; however, by limiting our summaries to investigations with the same sample size, we controlled for this issue directly. Finally, a formal meta-analysis would have further reduced our data set by approximately 30%. We note that using the entire data set (all 60 articles listed above) provided similar qualitative results as those presented below.

For each article, we first summarized a variety of information related to sampling design. We were interested in sampling concerns that occur when investigators test for area and edge effects (Connor and McCoy 1979; Horn et al. 2000; Mancke and Gavin 2000; Parker et al. 2005), particularly situations where area tests were confounded by potential edge effects, such that an observed area effect could not

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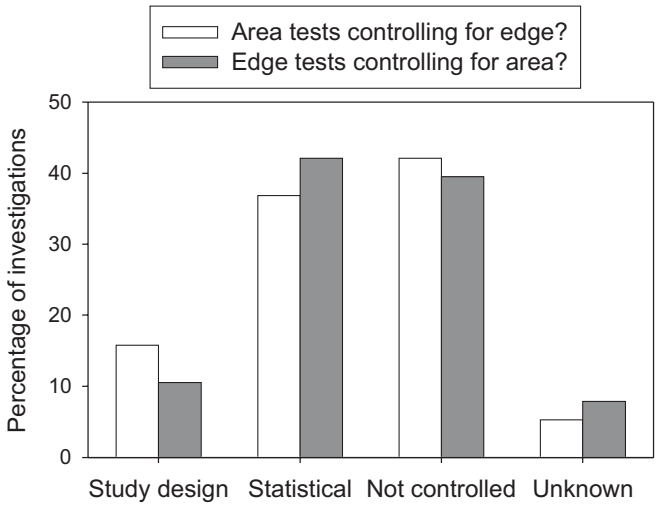
be inferred as a patch size effect. Parker et al. (2005) recently noted that most, if not all, studies on forest bird distribution in relation to area confounded potential area effects with edge effects because large patches had samples away from edges, whereas small patches inevitably did not. In contrast, similar studies focussing on edge effects tended to avoid such issues by selecting relatively large patches for comparisons (Parker et al. 2005). Here, we distinguish studies that control for these issues statistically, via covariates (e.g., Dunford et al. 2002) or residual analysis (e.g., Winter et al. 2000), those that control via study design (e.g., Wilder and Meikle 2005), and those that make no attempts to control for the confounding nature of area and edge (e.g., Hickerson et al. 2005). Study designs that we accepted as controlling for edge effects in tests of area included designs where samples were taken at the same distances from the nearest edge in patches of different sizes. While that approach does not control for multiple edges (Fig. 1; Fletcher 2005), in practice there are few ways to do so when testing for area effects. Study designs that we accepted as controlling for area when testing for edge effects included tests for edge within a given patch size class. Based on these classifications, we then compared conclusions from nonconfounded analyses to that of confounded analyses.

We report two main results for each response variable measured in the 38 studies. The first is whether significant effects were observed for edge, area, both, or neither. When observed for both, we report which effect was stronger based on inferential statistics provided in the article (e.g., *P* values, *F* statistics, confidence intervals), which is reasonable because we only considered studies with identical sample sizes for analyses of edge and area effects for a given response variable. The second main result is whether edge and area responses were concordant or discordant. We defined concordant responses as those where edge and area effects were observed in similar directions. For example, if the density of an organism declines near an edge (a negative edge effect; Ries et al. 2004) and declines in density with decreasing patch size (a positive area effect; Bender et al. 1998), then such responses would be concordant because habitat fragmentation generally increases the proportion of edge and decreases patch size. A concordant response suggests that habitat fragmentation has consistent effects on edge and area responses of a given variable and suggests four possible scenarios: (1) area and edge effects are driven by similar indirect processes (e.g., species interactions; Figs. 2*a*, 2*b*), (2) area effects may be explained simply by edge effects (particularly in confounded studies), (3) edge effects may be explained simply by patch size effects (particularly in confounded studies), or (4) our conceptual frameworks are incomplete and edge and area responses are, in fact, driven by some shared but unknown ecological mechanism. We only considered responses discordant if opposing patterns were observed for area and edge effects. Discordant results suggest that (*i*) edge effects do not drive observed area effects and that (*ii*) observed edge and area effects are generated by distinct ecological processes. We also note that the responses could be concordant or discordant as a result of chance alone. Mixed responses, where one effect was observed but the other was not, are difficult to interpret because low sample sizes may limit documenting area and (or) edge effects in some studies (e.g., Martínez-Morales 2005) and area effects are likely to be harder to detect as a result of larger site-to-site variation (see below). Therefore, we focus on concordant and discordant responses.

Fig. 3. Summary of investigations reviewed (n = 38) that did and did not attempt to control for the confounding nature of edge and area. We distinguished studies that control for these issues statistically, via covariates or residual analysis, those that control via study design, and those that make no attempts to control for the confounding nature of habitat area and edge. Only studies where the same response variable was tested for both factors were included. See text for details.



We stratified the results based on taxonomic group, the type of response variable investigated, focal habitats, and mechanisms tested. We summarized response variables into three general categories of metrics: community (species richness, diversity, or species composition), distribution (occurrence, abundance, or density), and performance (e.g., clutch size, survival). We examined coarse effects of habitat types that had adequate sample sizes, including grassland and forest. Few studies provided explicit information on landscape context, so we did not attempt to address this issue. Finally, we noted when investigators explicitly addressed potential mechanisms for edge and patch size effects and whether such mechanisms were supported. The review data set is available upon request from the senior author.

Review results and discussion

Many studies testing for edge and area effects were confounded in their design and (or) analysis, with similar confounding for tests of area (42%) and edge (39%; Fig. 3). Only 16 of the 38 articles (42%) controlled for both area and edge in at least some tests for a given response variable (nonconfounded analyses hereinafter). Many studies that addressed edge and area effects had "interior" plots that increase in distance from edge in larger patches (Hickerson et al. 2005; Weakland and Wood 2005), which confounds patch size and edge in tests of both. Investigations that did attempt to control for such issues predominantly did so with statistical tests rather than study design (Fig. 3). The studies we reviewed controlled for potential confounding more

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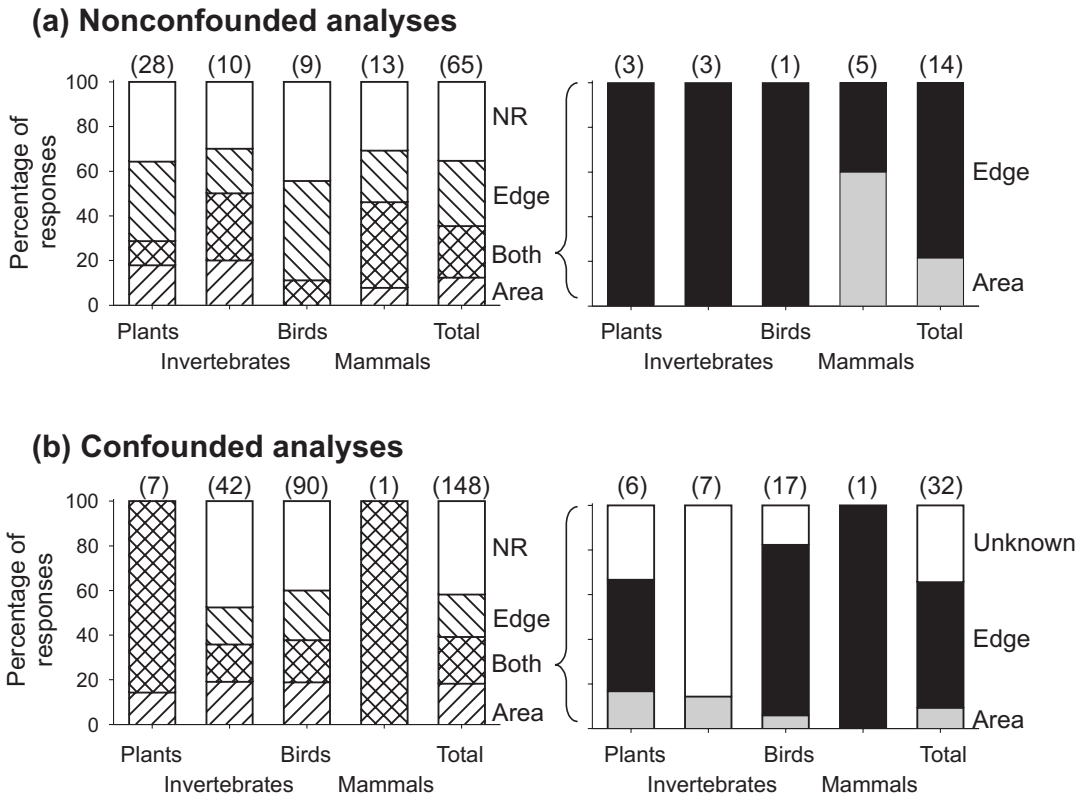
Fig. 4. Results from studies that tested for both edge and area effects on ecological patterns, summarized by taxonomic group for (*a*) nonconfounded analyses and (*b*) confounded analyses. Left panels show the percentage of response variables investigated that were influenced by area, edge, both edge and area (both), or had no reported effect (neutral response, NR), and numbers above bars represent the number of response variables investigated. Note that response variables for each taxa do not sum to the total because there were other taxa investigated that are not shown owing to limited sample size (e.g., herptiles). For those responses influenced by area and edge, the right panels show the percentage of response variables reported as being more influenced by edge or area (based on inferential statistics reported), and those that did not provide enough information to distinguish (unknown). For taxonomic groupings, we did not include studies that focussed on species interactions across different taxonomic groups. Only studies where the same response variable was tested for both factors were included.



often than those reported by Parker et al. (2005). This pattern is not surprising, because Parker et al. (2005) included many studies that only tested for either edge or area; such studies are more likely to be confounded than those testing for both effects. For further analyses, we compare these nonconfounded analyses to results from confounded analyses.

Nonconfounded analyses tended to find evidence for edge and area effects slightly more frequently (64.6%) than confounded analyses (58.1%; Fig. 4), with fewer nonsignificant responses reported. Sample size variation between confounded and nonconfounded analyses would actually predict the opposite, because overall sample sizes were greater for confounded analyses (nonconfounded: 61.3 ± 10.0, confounded: 95.7 ± 5.4; $t = 3.27$, $P = 0.001$). Confounded analyses reported edge and area effects in approximately equal proportions (39.9% vs. 39.2%, respectively; Fig. 4), while nonconfounded analyses found evidence for edge effects (52%) more often than area effects (35%). This pattern was generally similar regardless of the metric investigated (Fig. 5). Similar patterns also occurred for different habitats (Fig. 5), with edge effects being particularly common in grasslands. When both effects were observed, edge effects were stronger than area effects for nonconfounded analyses (78.6% vs. 21.4% of response variables, respectively) and confounded analyses (56.2% vs. 9.4% of response variables, respectively). The only exception was for investigations on mammals, with area effects being reported as stronger than edge effects for nonconfounded analyses (Fig. 4). Together, these results suggest that edge effects are either more common in nature or are easier to detect than area effects (or both). Edge effects may indeed be easier to detect because the most common study design, using within-patch measures of distances from edge, controls for site-level variation.

We caution that inferences about the relative occurrence and strength of edge versus area effects based on confounded studies differed from those based on nonconfounded studies. For example, nonconfounded investigations on birds found more evidence for edge effects, whereas confounded studies found similar evidence for area and edge effects (Fig. 4). Yet relatively few studies were not confounded, which limits generalizations for most taxa and highlights the need for rigorous study design and analysis in studies of habitat fragmentation.

There was a remarkable lack of discordance between observed area and edge effects, with only 1.6% of reported responses (1 of 64) for nonconfounded analyses and 2.4% (5 of 210; for 3 response variables, concordance–discordance could not be determined) for all studies combined showing

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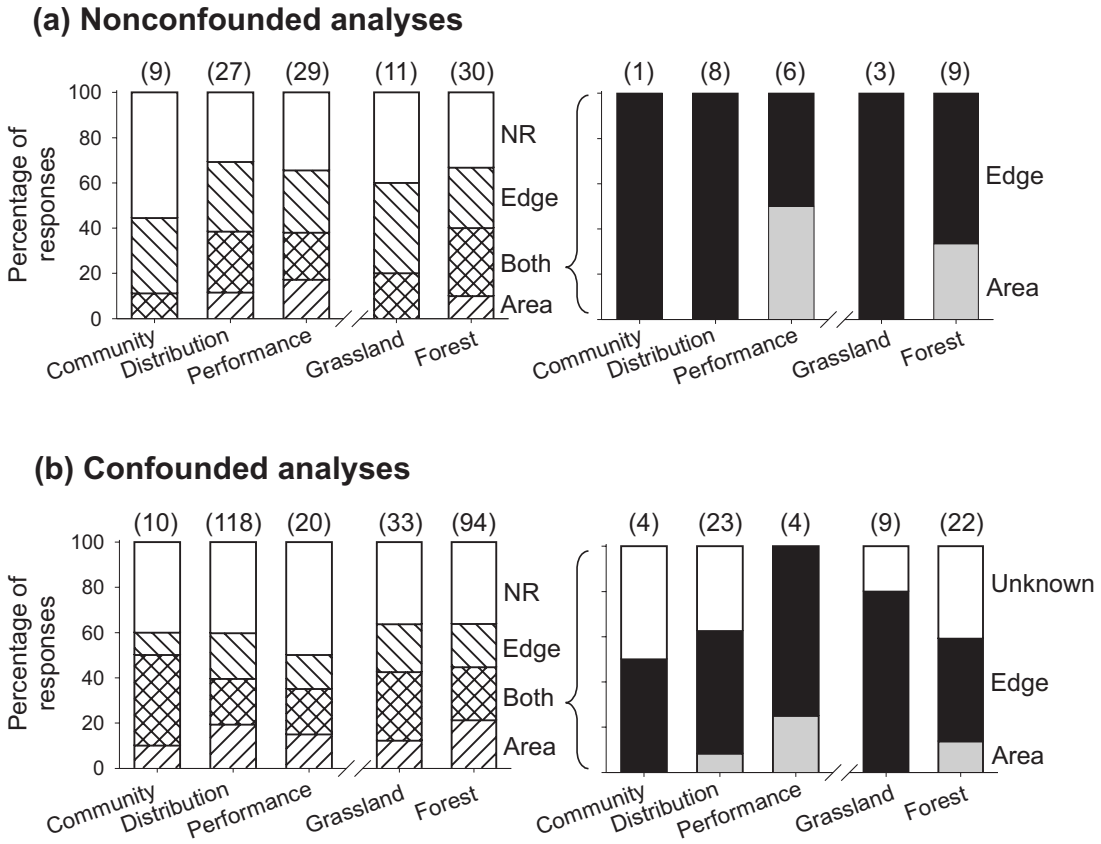
Fig. 5. Results from studies that explicitly tested for both edge and area effects on ecological patterns, summarized by metric used (distribution, community, performance) and habitat type (forest and grassland) for (*a*) nonconfounded analyses and (*b*) confounded analyses. Note that results for the metric used and habitat type separately summarize the same response variables. Format same as Fig. 4.



opposite patterns with respect to area and edge. The discordant responses were restricted to experiments on invertebrates in forested habitat (Davies and Margules 1998; Didham et al. 1998*a*). However, these results came from only two experiments, thus limiting our ability to assess the generality of the pattern. Concordance was observed for 57.8% of response variables in nonconfounded analyses (59.6% for confounded studies; Fig. 6). Given that discordance was rare (Fig. 6), that edge effects tended to be stronger when both effects were observed (Figs. 4, 5), and that nonconfounded analyses reported area effects less often and edge effects more often than confounded analyses (Fig. 4), we conclude that area effects reported by confounded studies may, in fact, often be the result of edge effects.

Relatively few studies explicitly tested for mechanisms generating edge or area effects (21.1%), with even fewer explicitly testing for mechanisms for both effects for at least one response variable (15.8% of studies reviewed). This was likely due, in part, to the difficulty of testing for mechanisms of both effects in a given investigation. Articles that did address mechanisms focussed on measures directly or indirectly related to resource mapping (Wilder and Meikle 2005) and (or) changes in species interactions (Storch 1991; Suarez et al. 1998; Lienert and Fischer 2003), both of which can occur from either edge or patch size effects (or both), thereby limiting inference about whether edge or patch size governed observed responses. None of these articles addressed the direct processes influenced by area and edge to interpret their unique contributions. We note that investigations focussing entirely on edge or area have addressed mechanisms responsible for potential effects more often (Ambuel and Temple 1983; Askins et al. 1987; McGeoch and Gaston 2000; Cronin 2003*a*; Fletcher and Koford 2003; Ries and Fagan 2003). Because of the confounding nature of these effects, any attempt to understand the mechanisms of edge or patch size should do so by explicitly searching for the direct effects of each landscape element (Fig. 2).

Future research: avoiding the pitfalls of confounding factors

The results of our review, as well as other studies, suggest that edge effects can sometimes explain area effects (Sisk et al. 1997; Laurance et al. 1998; Schtickzelle and Baguette 2003; Fletcher 2005), yet the converse is less likely based on the fundamental mechanisms influenced by patch size. For example, in a rigorous experiment on fragmentation, Bowers et al. (1996) suggested that space use and reproductive behaviors of female meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) near edges were responsible for the observed negative area effects (see also Wilder and Meikle 2005). Ambuel and Temple (1983) similarly invoked inter-

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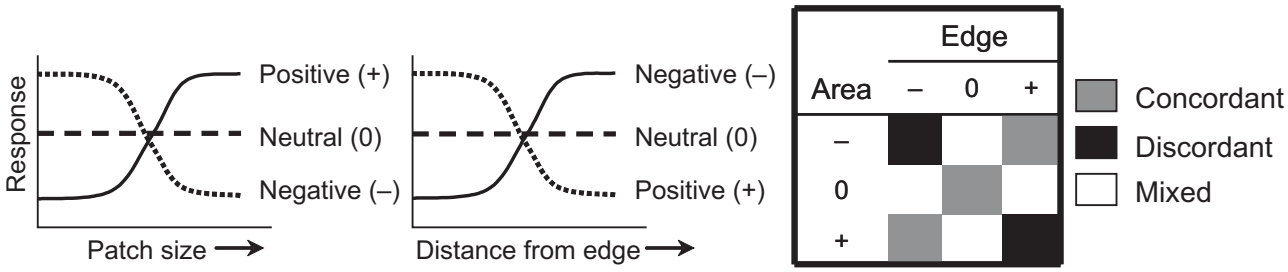
Fig. 6. Concordance of edge and area effects in fragmented landscapes for (*a*) nonconfounded analyses, (*b*) confounded analyses, and (*c*) all studies combined. Results are from studies that explicitly tested for both edge and area effects on ecological patterns. To be consistent with the literature, we report positive area effects as those that occur when the response variable increases with increasing patch size, whereas positive edge effects occur when a response variable increases near edges. Only studies where the same response variable was tested for both factors were included.



(a) Nonconfounded analyses

	Edge		
Area	**–**	**0**	**+**
–	1	1	7
0	13	23	5
+	7	7	0

(b) Confounded analyses

	Edge		
Area	**–**	**0**	**+**
–	2	5	6
0	16	62	12
+	19	22	2

(c) All analyses

	Edge		
Area	**–**	**0**	**+**
–	3	6	13
0	29	85	17
+	26	29	2

specific competition near edges as an explanation for observed area effects in migratory forest birds. As noted above, some edge effects can also explain other fragmentation effects, such as the use of conservation corridors (Haddad 1999; Levey et al. 2005). When patch size effects occur, however, edge effects are not explicitly predicted, either based on variation in resources influencing population size (MacArthur and Wilson 1967) or based on variation in emigration and immigration rates in patches that vary in size. Consequently, when investigators find support for both edge and area effects that are concordant in their directionality, and studies are confounded in their design and (or) analysis, such effects may be driven entirely by habitat edges alone (Laurance et al. 1998). When the strength of edge effects varies with patch size (Kiviniemi and Eriksson 2002), patch size effects could account for the additional variation. However, cumulative effects from multiple edges could also produce similar patterns (Fletcher 2005), thereby complicating the interpretation of the area–edge relationship.

The strongest study design for teasing apart the unique influence of area and edge occurs when investigators measure responses at similar distances from the nearest edge in fragments of different sizes, with replicates for each patch size category. Such a design controls for potential edge effects (from the nearest edge) in area tests, and potential area effects in edge tests, by addressing variation in edge effects across different patch sizes (see, e.g., Nour et al. 1993). Additionally, investigators can use statistical approaches to further limit confounding in this design (e.g., distances to multiple edges), whereas statistical approaches alone may be fruitless in limiting potential confounding for some other study designs.

Another approach to isolate the effect of area independent of edge is to compare predictions derived from edge responses to observed responses that occur with variation in patch size. The effective area model (Sisk et al. 1997; Brand et al. 2006) provides one approach to do so. In this model, response variables are estimated for different patches via data from edge transects. Edge response patterns measured at survey plots at different distances from habitat edges can be extrapolated to patches of different sizes to predict the average response in a patch that would result entirely from edge effects. When controlling for other site-level effects, consistent discrepancies between predictions from the effective area model and observed data as a function of patch size may be attributed to patch size and not edge effects.

We emphasize that focussing on the direct influences of habitat area and edge on ecological processes provides a more rigorous framework with which to understand the impacts of habitat fragmentation. Ries et al. (2004) argued that resource mapping and species interactions are the drivers of most observed edge effects, yet these can also vary with patch size (Fig. 2). Even though indirect effects from patch size and edge may be inevitably intertwined, making it difficult to isolate the effects of each landscape element, direct effects are distinct. Therefore, focussing on response variables that illuminate these direct effects will provide novel insight into the unique roles of area and edge. Our conceptual frameworks (Fig. 2; Ries et al. 2004) suggest that studies focussing primarily on movement in relation to edge and

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patch size can help to isolate the effects of these landscape elements. For instance, edge effects from ecological flows predict that organisms may change movement behaviors near habitat boundaries, whereas patch size should only influence the likelihood of encountering an edge. Likewise, patch size effects arising from "target" effects predict per capita immigration and emigration rates to vary with patch size but not with distance from edge. While there have been recent attempts to provide rigorous approaches to estimating movement in complex landscapes (Schtickzelle and Baguette 2003; Hamback and Englund 2005; Martin et al. 2006), none of the investigations we reviewed focussed on movement behaviors (e.g., encounter and turning rates) to disentangle the influence of both patch size and edge.

Conclusions

Habitat area and edge are key components of landscape structure, yet these components tend to covary within landscapes. Because habitat area and edge describe different aspects of landscape structure, the importance of each suggests different foci for conservation strategies, making it imperative to understand their unique roles in habitat fragmentation. Unfortunately, to date much of the literature testing for the influence of edge and area has been confounded. Information from nonconfounded studies suggests that edge effects may occur more frequently in nature than area effects. However, edge responses are likely easier to detect and our summaries made no attempt to measure overall effect sizes, such that area effects may, in some cases, be more important than these results suggest. In addition, we emphasize that variation in habitat area at landscape scales via habitat loss is widely known to be of considerable importance to population and community dynamics (e.g., Fahrig 1997; Flather and Bevers 2002). Future attempts to isolate edge and patch size effects need to pay careful attention to study design and focus on the direct, fundamental processes influenced by area and edge.

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Factors affecting butterfly use of filter strips in Midwestern USA

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Abstract

Filter strips are areas of herbaceous vegetation planted between agricultural fields and streams. In 2002 and 2003, the butterfly community in filter strips of a variety of widths and vegetative compositions was studied. Transect surveys were used to quantify butterfly abundance and diversity and measured vegetative variables in conjunction with each butterfly survey round. Overall butterfly diversity (H′) and abundance of habitat-sensitive butterflies were positively correlated with filter strip width. Using stepwise regression, the best models to explain butterfly abundance included the coverage of forbs and the number of ramets in bloom in the strips, and indicated positive relationships between forbs and the butterfly community ($R^2 = 0.33$ and 0.07, respectively). The models that best explained abundances of large, habitat-sensitive butterflies included the height and vertical density of vegetation. The planting of forbs in filter strips is rare, but may be useful for providing food sources to butterflies.
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Keywords: Butterflies; Community; Agricultural landscape; Filter strips

1. Introduction

Grassland in the Midwestern United States has been dramatically reduced in the past century as native vegetation was converted to rowcrop agriculture. In Minnesota, loss of tallgrass prairie has been estimated at 99.6% (Samson and Knopf, 1994). Federal land retirement programs, such as the Conservation Reserve Program (CRP), have re-established millions of hectares of grassland in the Midwest (Heard, 2000). Under these programs, farmers can be reimbursed for removing portions of land from crop production to plant grasses. In 1996, the United States Department of Agriculture (USDA) initiated continuous enrollment CRP (United States Congress, 1996). Several types of linear buffer plantings are eligible under this program. Whereas buffers are being established primarily to improve water quality and to control soil erosion, additional benefits gained from buffers may include enhanced aesthetics and wildlife habitat (Heard, 2000).

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The assumption that higher densities of animals in a given habitat type indicate superior habitat quality can be misleading (Van Horne, 1983; Pulliam, 1988; Pulliam and Danielson, 1991). The idea that low-quality corridors could act as ecological traps has been proposed (Anderson and Danielson, 1997), suggesting the need to assess the quality of potential stepping stone habitat to identify possible risks as well as benefits. Predation risk to butterflies could be elevated in narrow strips of habitat if the predators' efficiencies or abundances are higher in these areas. Other researchers have shown that bird abundances are often greater in strip-cover habitat than in surrounding rowcrop fields (Best et al., 1995), and sometimes greater than in surrounding block-shaped grassland areas (Best, 2000). In soybean fields in Ohio, researchers found that aboveground arthropod predators were higher in grassy corridors than in adjacent soybean fields; the corridors may have even drawn in predators from the planted fields (Kemp and Barrett, 1989).

This research examined butterfly community composition in a variety of different filter strip widths and plant compositions. The objectives were to (1) quantify the abundance and diversity of butterflies in filter strips and (2) assess the influence of filter strip width and vegetative composition on butterfly abundance and diversity.

2. Methods

The research focused on filter strips in a five-county area in southwest Minnesota (Jackson, Cottonwood, Watonwan, Nobles and Brown counties), which cover portions of the Minnesota River and Des Moines River watersheds. This region is dominated by corn and soybean production. Land in the area is primarily privately owned; less than 5% of land in any of these counties is state-owned (Minnesota House of Representatives, 2003).

Categorization of filter strips fell into three general planting types based on the seeding plans filed with the Natural Resources Conservation Service (NRCS): non-native, switchgrass (*Panicum virgatum*)-dominated and diverse mixtures of native species. Fourteen non-native, 14 switchgrass and 15 native strips were selected for use. Forty-nine filter strips were used in this study, all of which had been established for 3–7 years. Selected filter strips were planted on both sides of the streams that they buffer, were >350 m long and were bordered laterally by crops such as corn, soybeans or wheat. Filter strips did not differ significantly in their management. None were treated with insecticide or fertilized; usual techniques for weed control were infrequent spot mowing and spot spraying.

To reduce the number of confounding variables, only filter strips with either no trees or minimal numbers of trees growing in them were used. All trees present in the strips within 100 m of the transect were counted, and filter strips were placed into the following categories: no trees (30 strips), 1–10 trees (16 strips) or 11–50 trees (3 strips). A one-way analysis of variance (ANOVA) showed no difference in either the abundance ($F = 0.41$, $p = 0.66$) or the richness ($F = 1.17$, $p = 0.32$) of butterflies among the three categories.

Each site had one transect, and each transect, marked with pin flags, was 200 m × 5 m. Transects were placed in the middle of one side of each filter strip and began at least 50 m from any roadway adjacent to the strip. Butterfly surveys were timed to coincide with periods of greatest butterfly activity; they were conducted on warm (≥18 °C), sunny (<60% cloud cover) and calm (sustained winds <16 km/h) days between 09:00 and 17:30 h. Butterfly survey methods followed a modification of Thomas (1983). Transects were walked at a speed of 10 m/min; survey effort was constant at 20 min/transect. All butterflies within a 5 m × 5 m visual field in front of the observer were identified and their behavior was recorded. Timers were stopped for capture and recording. Any butterflies that observers were unable to identify in the field were captured using a net and transported to the lab in a glassine envelope for identification. To minimize observer bias, surveyors were rotated in each filter strip throughout the season. Two surveys occurred in 2002 (July 5–22 and July 22–August 15) and 2003 (June 16–July 12 and July 15–August 11).

To better understand the relationship between filter strips and the butterfly community, the butterfly species were separated into two guilds before conducting the analyses—disturbance-tolerant and habitat-sensitive (Table 1). Each species was categorized based upon information presented in Opler and Krizek (1984), Scott (1986), Glassberg (1999) and

Table 1
Numbers of individuals of each butterfly species observed during transect surveys of 49 filter strips during the summers of 2002 and 2003 in southwest Minnesota

Species	Number of individuals	Guild category
Everes comyntas (eastern tailed-blue)	537	Disturbance-tolerant
Danaus plexippus (monarch)	321	Disturbance-tolerant
Colias eurytheme/philodice (orange/clouded sulphurs)[a]	303	Disturbance-tolerant
Ancyloxypha numitor (least skipper)	118	Disturbance-tolerant
Speyeria idalia (regal fritillary)	90	Habitat-sensitive
Vanessa cardui (painted lady)	77	Disturbance-tolerant
Cercyonis pegala (common wood-nymph)	69	Habitat-sensitive
Vanessa atalanta (red admiral)	67	Disturbance-tolerant
Pieris rapae (cabbage white)	25	Disturbance-tolerant
Satyrodes eurydice (eyed brown)	17	Habitat-sensitive
Pholisora catullus (common sootywing)	15	Disturbance-tolerant
Anatrytone logan (Delaware skipper)	14	Habitat-sensitive
Papilio polyxenes (black swallowtail)	8	Disturbance-tolerant
Phyciodes tharos (pearl crescent)	6	Disturbance-tolerant
Speyeria cybele (great spangled fritillary)	6	Habitat-sensitive
Pyrgus communis (common checkered-skipper)	5	Habitat-sensitive
Limenitis archippus (viceroy)	4	Disturbance-tolerant
Polites peckius (Peck's skipper)	4	Disturbance-tolerant
Papilio glaucus (eastern tiger swallowtail)	3	N/A[b]
Lycaena hyllus (bronze copper)	2	Habitat-sensitive
Polites mystic (long dash)	2	Habitat-sensitive
Polites themistocles (tawny-edged skipper)	2	Disturbance-tolerant
Celastrina argiolus (spring azure)	1	Habitat-sensitive
Epargyreus clarus (silver-spotted skipper)	1	Disturbance-tolerant
Limenitis arthemis asyntax (red-spotted purple)	1	Disturbance-tolerant
Poanes hobomok (Hobomok skipper)	1	N/A[b]
Polites origines (crossline skipper)	1	Habitat-sensitive
Speyeria aphrodite (Aphrodite fritillary)	1	Habitat-sensitive
29 Total species	1701[c]	

Butterflies occurring commonly in anthropogenically disturbed areas are classified as disturbance-tolerant; species requiring unaltered habitat during any part of their life cycle are classified as habitat-sensitive.

[a] *Colias* spp. were combined due to initial identification uncertainty.

[b] Species adapted to woody habitats were not classified as disturbance-tolerant or habitat-sensitive.

[c] Does not include 88 individuals not identified to species.

Ries et al. (2001). Disturbance-tolerant butterflies are species that can be found commonly in areas altered by humans such as suburban lawns and gardens. Habitat-sensitive species have more specific requirements for habitat, either due to larval hostplant requirements or the needs of other life stages, and are often found only in relatively natural areas.

A vegetation survey was completed in conjunction with each round of butterfly surveys. Eleven 0.5 m × 0.5 m quadrats were regularly spaced every 20 m for the length of the transect. Estimation of the percentage of cover followed a modification of Daubenmire (1959) method using percentage cover as a continuous variable rather than percentage classes. At each quadrat, an observer estimated the coverage of all grass, all forbs, bare ground, standing dead vegetation and litter (hereafter all percentage cover estimates will be referred to as coverage). The grass coverage estimate was then further broken down into several component estimates: switchgrass, other natives, non-natives, wheatgrass and quackgrass (*Agropyron*) species and shoots. The coverage of switchgrass was estimated independently of other natives due to its preponderance in seeding plans. The coverage of *Agropyron* species was estimated independently because of the difficulty of distinguishing native species from non-native species in the field. This genus was therefore excluded from analyses

comparing relative coverages of non-native and native grasses.

Vegetation height and vertical density estimation followed a modification of Robel et al. (1970) method. An observer positioned at a distance of 1.5 m from a Robel pole and at a height of 1 m, recorded the maximum height of vegetation (live or dead) in front of the pole, and the minimum height at which visual obstruction of the pole was not complete. This measure provides an index of the vertical density of the vegetation.

Nectar availability in the strips was estimated by counting the numbers of ramets (stems emerging independently from the ground) in bloom in each quadrat. In 2003, the species richness of both forbs and grasses was also tallied for each quadrat. For those filter strips that had trees in them, the number of trees was estimated, as was the distance of the trees from the transect. Adjacent cover types were also recorded.

Width of each filter strip (both sides) was measured using a laser range finder at the beginning, middle and end of the transects, using the mean width value in all analyses. Width measurements were taken from aerial photos for those sites where lack of access or visual obstruction prevented the use of the range finder.

Butterfly abundance and Shannon–Weiner diversity (H') were calculated as means of all rounds, while species richness was tallied across rounds to arrive at a total number of species observed at each site over both years. Regression analyses were used to identify any relationships between filter strip width and butterfly abundance and diversity. The abundances of species with a sufficient sample size (>50 observations) were also used as a response variable in the analyses of width and vegetative composition.

All vegetation coverage data were expressed as proportions, and then transformed by taking the square roots, and then the arcsines. The 11 vegetative variables (coverage of switchgrass, coverage of other native grasses, coverage of non-native grasses, coverage of grass shoots, coverage of forbs, coverage of bare ground, coverage of standing dead vegetation, coverage of litter, number of ramets in bloom, vegetation height and vertical density) were analyzed using principal components analysis (PCA), conducted on the correlation matrix. The first four principal components, which all had eigenvalues greater than one, were rotated using varimax factor rotation (Cody and Smith, 1997), which allowed for a clearer interpretation of the loadings in the four axes (factors). These four rotated factors were then entered into a series of stepwise regressions (probability to enter = 0.15) to examine what factors might influence total butterfly abundance, diversity and the abundance and diversity of the disturbance-tolerant and habitat-sensitive butterfly guilds.

3. Results

Native species often observed in the filters strips included Canada wild rye (*Elymus canadensis*), Indiangrass (*Sorghastrum nutans*) and big and little bluestem (*Andropogon* spp.). Among the non-native grasses, smooth brome (*Bromus inermis*), reed canarygrass (*Phalaris arundinacea*) and quackgrass (*Agropyron repens*) were often present in filter strips. Common forbs in filter strips included Canada thistle (*Cirsium canadense*), alfalfa (*Medicago sativa*) and sweet clover (*Melilotus* spp.).

The planting type categories, which were determined a priori, contained significant variation in coverage of various vegetation elements. Thus, the categories primarily describe the most dominant vegetation in the strips. For example, the mean coverage of switchgrass among the 14 strips in the switchgrass-dominated treatment was 52%, and the mean coverage of non-native grasses in the 15 non-native strips was 56%. The analysis focused more on vegetation variables than planting type categorization because planting type did not always reflect realized vegetation composition.

Some counties within the study area had a higher prevalence of non-native filter strips, while others had more switchgrass filter strips. Likewise, some areas had more narrow strips and others had wider strips, depending on the availability of additional funding sources in the counties. However, for the strips in this study, filter strip width did not significantly differ among the three planting treatments ($F = 2.70$, $p = 0.08$).

Over the course of the summers of 2002 and 2003, 1789 individual butterflies of 29 species were observed in the filter strips (Table 1) and 1490 individuals of 16 species were observed in the disturbance-tolerant guild; the habitat-sensitive guild

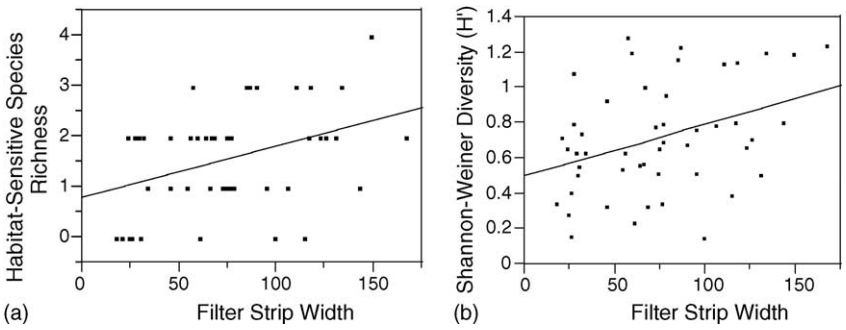

Fig. 1. Linear regressions of filter strip width (m) and response variables of the butterfly community surveyed during the summers of 2002–2003 in southwest Minnesota. Relationship between filter strip width and (a) species richness of habitat-sensitive butterflies (d.f. = 48, $R^2 = 0.15$, $p < 0.01$) and (b) Shannon–Weiner diversity of butterflies (d.f. = 48, $R^2 = 0.14$, $p < 0.01$).

had 207 individuals of 11 species. *Everes comyntas*, the eastern tailed-blue, was the most abundant species, accounting for 30% of the total abundance. The monarch (*Danaus plexippus*) and sulphurs (*Colias* spp.) were the next most abundant species, accounting for 19 and 18% of the total abundance, respectively (Table 1).

The width of filter strips used in the project ranged from 18 to 167 m. The diversity (H′) of butterflies in the sampled area was positively correlated with the width of filter strips (Fig. 1b, $R^2 = 0.14$, $p < 0.01$), but butterfly abundance was not ($R^2 = 0.01$, $p = 0.59$). The positive relationship between butterfly diversity and filter strip width was driven by the habitat-sensitive butterflies; abundance of habitat-sensitive butterflies was highly positively correlated with filter strip width ($R^2 = 0.14$, $p < 0.01$). Species richness of habitat-sensitive butterflies was also positively correlated with strip width (Fig. 1a, $R^2 = 0.15$, $p < 0.01$). By contrast, species richness of disturbance-tolerant butterflies was not correlated with filter strip width ($R^2 = 0.03$, $p = 0.21$). Larger species in the Nymphalidae family were more sensitive to filter strip width than other species. Of the eight species analyzed individually, *D. plexippus*, *S. idalia* and *V. atalanta* were positively correlated with filter strip width (Table 2).

Butterfly abundance and richness as well as the abundance of the eight individual species were examined with respect to the four rotated vegetation factors from the PCA. Butterfly abundance and disturbance-tolerant abundance were best explained by factor 3 (Table 3), a linear combination of forb cover and the number of ramets in bloom (Table 4). Habitat-sensitive species abundance was best explained by factor 1, a combination of the vertical

Table 2
Responses of the eight most abundant species R^2 values from regressions on mean abundances with rotated vegetation factors and width

Species	Factor 1	+/−	Factor 2	+/−	Factor 3	+/−	Factor 4	+/−	Width	+/−
A. numitor	0.0015		0.1657**	−	0.2578***	−	0.0075		0.03	
C. eurytheme	0.0277		0.0392		0.0561		0.0499		0.02	
D. plexippus	0.0147		0.0024		0.0003		0		0.26**	+
E. comyntas	0.0229		0.0089		0.3776***	−	0.0079		0.05	
V. atalanta	0.0015		0.0032		0.0011		0.0112		0.11*	+
V. cardui	0.0070		0.0150		0.0066		0.1215*	−	0.01	
C. pegala	0.0808*	−	0.0004		0.0100		0.0833*	−	0.02	
S. idalia	0.1220*	−	0.0157		0.0017		0.0020		0.15**	+

d.f. = 48. See Table 4 for interpretation of variables.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.0010$.

Table 3
Results of stepwise regressions on abundance and species richness of all butterflies and of the two guilds, disturbance-tolerant (DT) and habitat-sensitive (HS) butterflies

Butterfly variables	d.f.	R^2	Variables in best model	Direction of relationship
Total abundance	48	0.33[a]	Factor 3	Negative
HS abundance	48	0.12[b]	Factor 1	Negative
DT abundance	48	0.32[a]	Factor 3	Negative
Total richness	48	0.05	Factor 3	Negative
HS richness	48	0.07	Factor 1	Negative
DT richness	48	0.07	Factor 3	Negative

[a] Indicates significance at the $p < 0.001$ level.
[b] Indicates significance at the $p < 0.05$ level.

density and height of the vegetation and percent switchgrass.

The analysis of individual species' abundances with the vegetation factors demonstrated an inconsistent response across families, guilds and sizes (Table 2). The only species that were correlated with factor 1 were two habitat-sensitive species. Abundances of *C. pegala* and *S. idalia*, both larger grassland butterflies, were negatively correlated with factor 1 (Table 2), indicating positive relationships with the height and vertical density of vegetation (Table 4). *A. numitor*, a small, disturbance-tolerant skipper, was the only species found to be correlated with factor 2 (Table 2). This negative relationship represents a positive association with coverage of non-native grasses and a negative correlation with coverage of shoots (Table 4). The abundances of two small, disturbance-tolerant species, *A. numitor* and *E. comyntas*, were negatively correlated with factor 3 (Table 2), indicating a positive relationship between the abundances of these species and the coverage of forbs and the number of ramets in bloom (Table 4). The abundances of *V. cardui* and *C. pegala* were negatively correlated with factor 4 (Table 2), indicating a negative relationship with standing dead vegetation, and a positive correlation with coverage of native grass (Table 4).

Table 4
Rotated factor loadings from a principal components analysis of vegetation variables

	Factor 1	Factor 2	Factor 3	Factor 4
Switchgrass (%)	**−0.80**	0.24	0.34	0.19
Native grass (%)	0.09	0.48	0.19	**−0.65**
Non-native grass (%)	0.54	**−0.74**	−0.08	0.04
Shoots (%)	−0.09	**0.80**	−0.14	0.02
Forbs (%)	0.02	0.33	**−0.83**	−0.14
Bare ground (%)	0.23	**0.72**	−0.37	−0.05
Litter (%)	0.45	−0.07	0.06	0.34
Standing dead vegetation (%)	−0.12	0.14	0.20	**0.77**
Number of ramets in bloom	0.00	0.01	**−0.91**	0.00
Vertical density	**−0.94**	−0.11	0.08	0.07
Vegetation height	**−0.83**	0.01	−0.16	0.11

Loadings that we consider to be the most important to a factor are in bold.

4. Discussion

Abundance and richness of habitat-sensitive butterflies was positively correlated with filter strip width. Thus, species adapted to tallgrass prairie and sensitive to disturbance may not benefit from narrow plantings. The relationship between filter strip width and the butterfly community is more complicated; however, overall butterfly abundance was not correlated with filter strip width. This result was especially unexpected given the large range of widths addressed by this study (18–167 m). To the human eye, a filter strip 18 m wide appears as an insignificant band of grass, while a strip 170 m wide seems a substantial area of habitat in which one might reasonably expect to encounter even large mammalian wildlife. An examination of sensitivity to width also demonstrates that larger brushfoots (Nymphalidae) have higher abundances in wider strips. *D. plexippus*, *S. idalia* and *V. atalanta* are all large butterflies and strong fliers, but they have very different habitat requirements. *S. idalia* is habitat-sensitive and has been shown to be responsive to habitat edges, contrasting sharply with *D. plexippus*, a disturbance-tolerant generalist which is unaffected by grassland-crop edges (Ries and Debinski, 2001).

The results highlight the importance of flowering plants to butterflies, and bring into focus an opportunity to improve filter strips as butterfly habitat. The use of forbs as part of the seed mix for filter strips is rare. Approximately 11% of the filter strips identified as potential study sites contained forbs in the planting plan, and half of those list only sweet clover (*Melilotus* spp.). There are several potential reasons for this. Planting native forbs is more expensive than planting just grass. The 2004 online catalog for Ion Exchange, a large Midwestern prairie seed company, charges US$ 10/lb for a mix of native grasses and US$ 100/lb for its ''butterfly/hummingbird prairie mix'' which adds 26 forb species. Thus, the landowner may have to pay a significant premium to have forbs in his/her filter strip. Secondly, invasion of filter strips by Canada thistle (*Cirsium canadense*), a noxious weed, is a widespread problem; the NRCS requires landowners to mow or spray problem areas. For many farmers, the easiest way to control thistles is to spray the filter strip with an herbicide designed to specifically kill broad-leaved plants (it does not affect grasses). This type of treatment obviously kills forbs intentionally planted as well as the thistles. An additional barrier to planting forbs is that the primary function of filter strips is water filtration; creation of butterfly habitat is a secondary benefit.

The positive relationship between abundance of habitat-sensitive species and specifically larger grassland butterflies such as *C. pegala* and *S. idalia*, with the height and vertical density of vegetation also makes sense. These species may need tallgrass to provide habitat structure, and a variety of microhabitat conditions. On hot, sunny midafternoons, many butterflies stay deep in the vegetation, potentially to find shade or moisture.

The analysis of how the eight most abundant species respond to filter strip width and vegetation yielded a wide array of relationships. Given that the overall butterfly community responds positively to forb coverage, the lack of a consistent response to forbs amongst the eight most abundant species was somewhat surprising. The fact that the two species which exhibited a positive relationship with forbs were the two smallest species observed in the transects (*E. comyntas* and *A. numitor*) may help explain these findings; the correlation may be due to higher energy demands in smaller butterflies, which could cause these butterflies to remain in close proximity to nectar sources. To examine whether the strong relationship with forbs was being driven by the most abundant species in the surveys, *E. comyntas* was removed from the dataset and a new analysis was conducted. Butterfly abundance without *E. comyntas* was positively correlated with coverage of forbs (d.f. = 48, $R^2 = 0.18$, $p = 0.0024$). Thus, although the response was not consistent across all species, the majority of the butterfly community exhibits a positive relationship with coverage of forbs.

This research indicates that even narrow filter strips were used by butterflies. However, wider plantings support a higher diversity of butterflies, as well as larger abundances of habitat-sensitive butterflies. Therefore, increased filter strip width may appeal to managers wishing to provide habitat for species beyond those seen in suburban yards. Increasing the vegetation height and vertical density may also influence the richness of such habitat-sensitive species. Abundances of forbs and the availability of nectar resources may affect a filter strip's ability to support a higher abundance of butterflies overall. Thus, enhancing filter strips by the use of wider plantings consisting of more warm-season grasses (which tend to be taller) and forbs should be accomplished whenever financially possible.

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Conservation Value of Roadside Prairie Restoration to Butterfly Communities

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Abstract: *It has been suggested that restoration of roadsides to native habitat can benefit wildlife by adding habitat and restoring connectivity between fragmented reserves. In Iowa, which has one of the highest road densities in the United States, roadside vegetation has traditionally been managed to maintain a monoculture of exotic grass. Recently, several Iowa counties have begun integrated roadside vegetation management, a program that both restores roadsides to native prairie vegetation and restricts the use of herbicides and mowing. We evaluated the effect of this management regime on butterfly populations along central Iowa roadsides. We surveyed 12 separate prairie roadside areas, comparing the abundance and species richness of disturbance-tolerant and habitat-sensitive butterflies in roadside prairies with those of nearby roadsides dominated by either weeds (primarily non-native legumes) or non-native grasses. We found that management of roadsides profoundly affected the butterfly community. Species richness of habitat-sensitive butterflies showed a two-fold increase in prairie compared with grassy and weedy roadsides ($p < 0.0001$), and abundance increased almost five times more on the prairie than on grassy roadsides ($p < 0.02$). Species richness of disturbance-tolerant butterflies showed no response to roadside management, although abundance was slightly higher in weedy and prairie roadsides than on grassy roadsides ($p < 0.01$). Of all habitat variables explored, the species richness of plants in flower showed the strongest effect on mean richness and abundance of both disturbance-tolerant and habitat-sensitive butterfly species. Although there were higher concentrations of road-killed butterflies near weedy and prairie roadsides than on grassy roadsides, relative numbers indicated that mortality risk was more than twice as high on grassy roadsides ($p < 0.0001$). Tracking studies showed that butterflies were less likely to exit prairie roadsides, indicating that their mortality rates may be lower and offering preliminary evidence that roadsides have the potential to be used as corridors. Overall, our results indicate that roadside restoration benefits butterfly populations. More detailed demographic data are necessary, however, to explore the possibility that roadsides are acting as sink habitat for some habitat-restricted species.*

Valor de la Conservación de la Restauración de Praderas Ruderales para Comunidades de Mariposas

Resumen: *Se ha sugerido que la restauración del hábitat nativo de los bordes de caminos puede ser benéfica para la vida silvestre al añadir hábitat y restaurar la conectividad entre reservas fragmentadas. En Iowa, con una de las densidades de carreteras más alta en los Estados Unidos, la vegetación ruderal tradicionalmente se ha manejado para mantener un monocultivo de pasto exótico. Recientemente, varios condados en Iowa han iniciado un programa de manejo integrado de la vegetación ruderal enfocado tanto a restaurar la vegetación de pradera nativa en los bordes de caminos como a restringir el uso de herbicidas y podas. Evaluamos el efecto de este régimen de manejo sobre poblaciones de mariposas a lo largo de carreteras en Iowa central. Examinamos 12 áreas de praderas ruderales separadas y comparamos la abundancia y la riqueza de especies de mariposas tolerantes a la perturbación y sensibles al hábitat en praderas ruderales dominadas por hierbas (principalmente leguminosas introducidas) o por pastos exóticos. El manejo de bordes de caminos afectó significativamente a la comunidad de mariposas. La riqueza de especies de mariposas sensibles al hábitat fue el doble en praderas que en bordes dominados por hierbas ($p < 0.0001$) y la abundancia fue casi cinco veces mayor en praderas comparadas con bordes con pastos ($p < 0.02$). La riqueza de especies de mari-*

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posas tolerantes a la perturbación no mostró respuesta al manejo de bordes de camino, aunque la abundancia fue ligeramente mayor en bordes con hierbas y con praderas comparados con bordes con pastos ($p < 0.01$*). De las variables del hábitat analizadas, la riqueza de especies de plantas con flor tuvo el mayor efecto sobre la riqueza y abundancia promedio de especies de mariposas tanto las tolerantes a la perturbación como las sensibles al hábitat. Aunque hubo mayor concentración de mariposas muertas por colisión cerca de bordes con hierbas y con praderas en comparación con bordes con pastos, los valores relativos indicaron que el riesgo de morir fue más del doble en los bordes con pastos (*$p < 0.0001$*). Estudios de localización mostraron que la probabilidad de que las mariposas salgan de los bordes con pradera es baja, lo que indica que las tasas de mortalidad pueden ser menores y ofrece evidencia preliminar de que los bordes de camino tienen el potencial de ser utilizados como corredores. En general, nuestros resultados indican que la restauración de bordes es benéfica para las poblaciones de mariposas. Sin embargo, se requieren datos demográficos más detallados para explorar la posibilidad de que los bordes de camino actúan como hábitat receptor para algunas especies de hábitat restringido.*

Introduction

Since the development of island biogeography theory (MacArthur & Wilson 1963), the ability of an increasingly fragmented system of natural reserves to support viable populations or retain species diversity for extended periods has been questioned (Diamond 1975). The problem is not just loss of habitat but isolation, which puts populations at greater risk of local extinction (Brown & Kodric-Brown 1977; Lande 1988; Saccheri et al. 1998). Roadside vegetation, which occupies approximately 8 million ha of land (Adams & Geis 1983) bordering nearly 6.4 million km of road in the United States (U.S. Department of Transportation 1998), has been suggested as a resource to both add habitat and restore connectivity between fragmented reserves (Bennett 1991; Spellerberg 1998).

Although the presence of roads is often considered to have negative effects on wildlife, the amount of land dedicated to roadside vegetation is substantial. For many regions where habitat loss has been severe and human presence is well established, roadside restoration offers an opportunity for extensive additions to the regional system of reserves. Therefore, information on the effects of roadsides on wildlife is crucial. Recently, many states have instituted policies to restore roadsides to native vegetation, often for the primary purpose of weed and erosion control (Henderson 2000). Although several studies have documented the use of roadsides by wildlife, we were not able to find a single study that examined the effect on any animal species of restoring roadsides to native habitat. The purpose of our study was to explore the conservation value of restored and native prairie roadsides to butterflies in central Iowa.

Roadsides as Additional Habitat

Several small-bodied animals, including birds (Laursen 1981; Arnold & Weeldenburg 1990; Cale 1990; Warner et al.1992; Camp & Best 1994), small mammals (Getz et al. 1978; Woodward 1990; Clark et al. 1996; Kirsch 1997), insects (Munguira & Thomas 1992; DeMers 1993; Vermeulen 1993; Eversham & Telfer 1994; Samways et al. 1997), snails (Baur & Baur 1992), and reptiles and amphibians (Way 1977; Seabrook & Dettmann 1996) use roadside vegetation as habitat. Most of the species found in this habitat are common (Bennett 1991), however, and the possibility that roadsides act as population sinks (Pulliam 1988) is rarely explored (Eversham & Telfer 1994). Source-sink dynamics in roadsides may have serious implications for the conservation of species on a regional scale because increasing the amount of sink habitat relative to source habitat in the landscape has the potential to decrease the overall population size, even as the amount of total habitat increases (Danielson 1992).

There are several negative consequences of using roadside vegetation as habitat. Approximately one million vertebrates are killed every day by cars in the United States (Lalo 1987), although some studies suggest that mortality from vehicles is only a minor contributor to overall death rates (Bennett 1991). Little research has focused on invertebrates, but one study found road mortality for butterflies to be high, yet minor compared with other causes (Munguira & Thomas 1992). Roads may be a barrier for dispersal (Mader 1984; Merriam et al. 1989), and culverts have been used to increase permeability (Yanes et al. 1995). Roadsides are also subject to contamination from passing cars, with high concentrations of several heavy metals being found in soil, vegetation, earthworms, and small mammals (Scanlon 1987).

Roadsides as Corridors or Stepping Stones between Habitat

The idea that corridors or "stepping stones" between habitat "islands" can decrease isolation of fragmented habitat has become extremely popular (Noss & Harris 1986; Noss 1987; Mann & Plummer 1993). Stepping stones provide small habitat patches between larger reserves that decrease the average distance between patches and therefore may decrease isolation. Habitat corridors are meant to directly connect habitat, but the idea remains controversial (Simberloff et al. 1992; Rosenberg et al. 1997).

One of the main criticisms of corridors is that the high cost of creating them could be better spent on other conservation priorities (Mann & Plummer 1993). Roadside vegetation is a permanent part of the landscape, however, and is already being actively managed. If corridors are a useful tool for conservation, roadsides may offer a source of corridor habitat that does not take resources away from other programs. Movements of organisms along roadside vegetation have been documented for several species (Suckling 1984; Arnold & Weeldenburg 1990; Bennett 1990; Vermeulen 1994). Roadsides have also been implicated as a factor in range expansion for mice (Getz et al. 1978) and ants (DeMers 1993). As with most proposed corridor systems, however, there is no direct evidence that roadsides accomplish the main goal of corridors: to reduce isolation of populations in larger habitat patches or reserves.

Prairies and Roadside Management in Iowa

Prairie is one of the most endangered ecosystems in the United States (Smith 1981). The tallgrass prairie has suffered the most severe decline, with a total loss of area estimated from 82% to 99%, more than any other major ecosystem in North America. Iowa is one of the most severely affected states, with <0.01% of the original tallgrass prairie remaining (Sampson & Knopf 1994). There are an estimated 179,000 km of roads in Iowa encompassing 243,000 ha of land (Flynn 1994). Traditionally, these roadsides were managed with aggressive mowing and spraying techniques to control invasive weeds. Recently, however, several Iowa counties have begun integrated roadside vegetation management (IRVM) programs that involve restoring roadsides to native vegetation and restricting the use of herbicides (Cramer 1991; Flynn 1994). Although IRVM is generally implemented for the purpose of weed and erosion control, another explicit goal of the program is to benefit wildlife (Cramer 1991). The uneven implementation of IRVM, both within and among counties, has resulted in a great deal of variation in the quality of roadsides in Iowa. Most roadside vegetation in central Iowa remains a uniform monoculture of exotic, cool-season grasses (primarily *Bromus* spp.), but many areas now have thickets of non-native flowers, and a small but growing number of roadsides are now dominated by native prairie grasses and wildflowers.

Status of Grassland Butterflies in Iowa

The health of an ecological system can often be gauged by its assemblage of species. Butterflies are a particularly useful group in this regard because they display a wide range of tolerances to habitat disturbance, are relatively well known, and their host-plant relationships are well described (Scott 1986). Many of the plants included in native seeding projects along Iowa roadsides serve as larval host plants or nectar resources for several species of butterfly.

The Iowa Natural Resource Commission lists 2 species of Iowa butterflies as endangered, 5 as threatened, and 25 as species of special concern. Schlict and Orwig (1998) have expanded this list to include 8 critically endangered species (known in only one to five sites), 15 endangered, and 21 threatened. They also list one butterfly, the Dakota skipper (*Hesperia dacotae*), a prairie specialist, as extinct in Iowa. Of the 44 species included on their list, 21 are considered prairie specialists.

Objectives

The goal of this study was to assess the effects of IRVM practices on butterfly communities. Our specific objectives were to (1) determine how IRVM affects butterfly communities, (2) compare butterfly communities in native and restored prairie roadsides, (3) compare butterfly communities in prairie roadsides with those in native, nonroadside prairie remnants, and (4) estimate the effect of butterfly mortality due to collisions with cars in different roadside habitats. We surveyed butterflies that overwinter in Iowa and that are associated with open habitat. Species that don't overwinter in Iowa move great distances during their lifetime and are not as strongly tied to local habitat patches. We divided species into those that are tolerant of highly disturbed habitat (disturbance-tolerant) and those that are not (habitat-sensitive). By focusing on species richness and the abundance of these two groups of butterflies, we show how management techniques may increase the value of roadside vegetation for butterfly populations.

Methods

Site Selection and Description

Each study area was located near a restored or native (never plowed) roadside prairie in central Iowa. We selected prairie roadside locations based on information gathered from county roadside managers in the four counties included in the study. The study included all high-quality restored roadsides that were at least 0.5 km long and well established. The length of restored roadsides varied considerably, ranging from a half kilometer to several kilometers. We also included all known native prairie roadsides located within the study area. In total, 12 study areas were established (Fig. 1), 4 areas with native roadsides and 8 with restored roadsides.

In all areas, each 160-m section of roadside vegetation within 1.6 km of the roadside prairie was classified as weedy (>20% non-native legumes), grassy (<5% forb cover and dominated by non-native grass, primarily *Bromus* sp.), or prairie (dominated by native prairie grasses

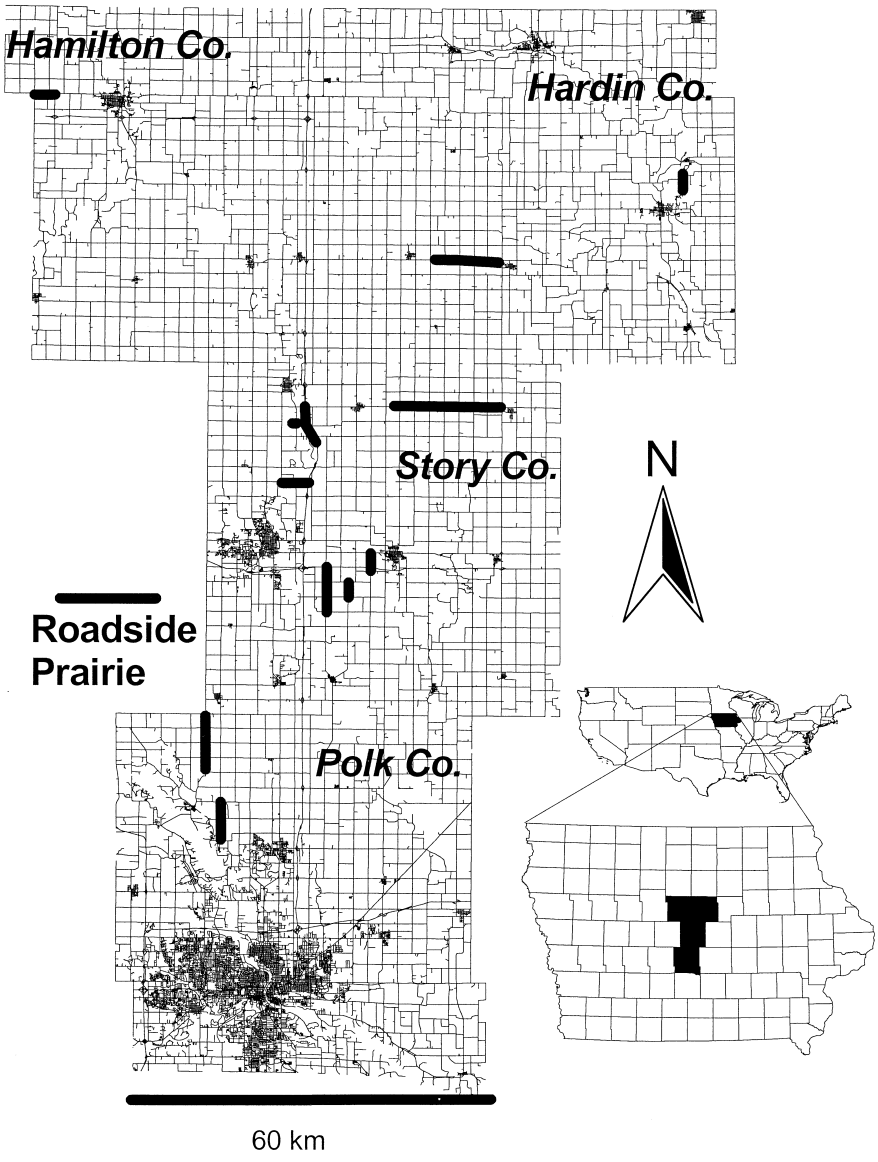

Figure 1. Map of study areas showing locations of roadside prairie restoration in four counties in central Iowa (U.S.).

and forbs). Weedy roadsides were restricted to those dominated by non-native legumes because their presence is tolerated by roadside managers. Other weeds, such as Canada thistle (*Cirsium arvense*), are considered nuisances and are subjected to intensive spot spraying or mowing (Cramer 1991).

Three plots were established within each roadside class (grassy, weedy, and prairie) within each area. Plot locations were randomly selected among plots that met the following requirements: at least 50 m away from all other plots, roadside at least 6 m wide and not dominated by wetland vegetation, grassy plots never adjacent to weedy plots, and both grassy and weedy plots at least 500 m from prairie plots to avoid spillover of individuals. All roadsides were bordered by row crops. Depending on the prevalence of grassy and weedy roadsides, some areas were missing either one or two plots. Of the 12 study areas (Fig. 1), 7 were complete and 5 were missing either 1 or 2 plots, resulting in a total of 101 study plots. The plots were located along a wide range of roads, from county gravel roads to interstate highways. Each survey plot was 50 m long and 5 m wide. To examine the differences between native prairie reserves and prairie roadsides, we established three randomly placed 50 × 5 m plots in four native prairie remnants ranging in size from 2 to 16 ha.

Butterfly and Flower Surveys

Three rounds of surveys, each lasting approximately 3 weeks, were conducted from 22 June through 22 August 1998. During the three rounds, each plot was visited three times, so over the course of the summer most plots were sampled nine times. Exceptions were plots that were

flooded or recently mowed. Within each area and round, the order in which surveys were conducted was random. Surveys were conducted between 1000 and 1830 hours when the temperature was between 21° and 35° C and sustained winds were below 16 km/hour. On partly cloudy days, surveys were started only when the sun was shining. Each transect was walked for 5 minutes in one direction; timers were stopped when a butterfly was seen. We conducted a total of 953 surveys over the summer.

During each survey, we counted all butterflies (including skippers) that overwinter in Iowa. Butterflies were identified on the wing if possible, otherwise they were netted. Due to the difficulty of identification in the field, *Colias eurytheme* and *C. philodice* were identified to genus and were considered one species throughout the analysis. Both species are common in Iowa and have similar host-plant specificity and disturbance tolerance (Scott 1986). The percent cover of flowers was estimated once during each round to determine the amount of nectar available to butterflies. Within each plot, six 5 × 1 m transects perpendicular to the butterfly transect were placed every 10 m. These 5 × 1 m transects were then broken down into 1 × 1 m sections. A visual estimate of the percent cover of the flowers of each species was made in each of the 30 1 × 1 m plots. The values were then averaged over the entire plot. Although somewhat subjective, this allowed us to obtain a relative measure of flower cover between plots in a manner that was not prohibitively time consuming.

Mortality Surveys

Mortality data were collected in two ways: observing movement behavior near roads and collecting dead butterflies along roadsides. Behavioral butterfly surveys were conducted only during the second round of sampling. Butterflies in the plot were observed for successful road crossings. A 50 × 2 m transect parallel to the study plots described previously, but with half the width of the plot extending into the road, was used for observation.

Each entry of a butterfly into the plot was classified either as an approach (butterfly entered the 1 m of vegetation but did not continue into the road); an attempt (entered plot, flew across part of the road or shoulder, but then turned back); or a cross (entered the plot from the vegetation and crossed the road). Individuals that crossed were further classified as to whether they succeeded in crossing the road or were struck and killed by a vehicle. Butterflies that flew perpendicular to the road were not used in the analysis. Seventy-five behavioral surveys were conducted.

Roadkill surveys were conducted after all regular butterfly surveys during the last two rounds. Transects in these surveys were parallel to each survey plot along both sides of the road's edge where the vegetation met the pavement or gravel. Again, only species that overwinter in Iowa were counted in the survey. Butterflies struck by cars rarely stuck in grills; in general, they became caught at the grass' edge within 25 m from the point of collision (personal observation). We conducted a total of 212 mortality surveys.

Data Analysis

For the community analysis, all butterflies observed were classified either as disturbance-tolerant or habitat-sensitive, based on data collected by the Iowa Lepidopterist Project (Nekola 1995) and habitat classifications given by Scott (1986). These categories were relative to the extreme level of habitat disturbance that occurs throughout Iowa, so species classified as disturbance-tolerant were those that survive well on farmland or within cities and towns. Species classified as habitat-sensitive were associated with areas that didn't receive high levels of continual human disturbance, but there was no requirement that they rely on native habitat. To calculate abundance, the mean for each of the three surveys conducted within one round was used to arrive at one value for each plot in each area. Plots of a single type within an area were considered subsamples and were averaged together to arrive at a single mean for grassy, weedy, and prairie roadsides for each of the 12 study areas. We used the same procedure for species richness but used the cumulative richness over three surveys before averaging values from different plots together within a study area. This procedure eliminated the problem of pseudoreplication (Hurlbert 1984).

For most analyses, the response variables examined were the number of species (species richness) and abundance for both disturbance-tolerant and habitat-sensitive butterflies. An analysis of variance (ANOVA) (PROC GLM; SAS Institute 1990) was used to compare abundance and species richness in grassy, weedy, and prairie roadsides. For the main analysis, restored and native roadsides were considered one type (prairie roadsides) because each of the 12 study areas acted as a "replicate" where all three roadside types were present, but no areas had both restored and native prairie roadsides. We used a separate *t* test to look for differences between native and restored roadsides and between prairie roadsides and nonroadside prairie remnants. We used ANOVA to test the effect of restoration size on butterfly abundance and richness using only prairie roadside plots. To examine this variable, we classified all roadsides as either small (<800 m in length), medium (800–5000 m), or large (>5000 m). We used linear regression to test for effects of flower cover and richness, but we analyzed each survey separately because flower abundance and diversity varied within areas and between rounds.

For the mortality survey, the number of individuals found dead along roads was divided by the number counted during the normal butterfly survey to obtain relative mortality rates. We used ANOVA to test for differ-

Table 1. Habitat category and total number of each species of nonmigratory butterflies observed during surveys of roadsides and prairies in central Iowa in 1998.

Common name	*Scientific name*	*Habitat category*[a]	*Number*
Sulpher	*Colias* sp.	disturbance-tolerant	1124
Eastern-tailed blue	*Everes comyntas*	disturbance-tolerant	1124
Pearl crescent	*Phyciodes tharos*	habitat-sensitive	710
Least skipperling	*Ancyloxypha numitor*	habitat-sensitive	170
Black swallowtail	*Papilio polyxenes*	disturbance-tolerant	145
Deleware skipper	*Atrytone logan*	habitat-sensitive	133
Common sootywing	*Pholisora catullus*	disturbance-tolerant	126
Cabbage white[b]	*Pieris rapae*	disturbance-tolerant	103
Common wood nymph	*Cercyonis pegala*	habitat-sensitive	77
Great spangled fritillary	*Speyeria cybele*	habitat-sensitive	48
Great grey copper	*Lycaena xanthoides*	habitat-sensitive	40
Red admiral	*Vanessa atalanta*	disturbance-tolerant	16
Viceroy	*Limenitis archippus*	habitat-sensitive	15
Yellow-patch skipper	*Polites peckius*	habitat-sensitive	14
Tiger swallowtail	*Papilio glaucus*	habitat-sensitive	13
Checkered skipper	*Pyrgus communis*	disturbance-tolerant	11
Two-spotted skipper	*Euphyes bimacula*	habitat-sensitive	10
Regal fritillary[c]	*Speyeria idalia*	habitat-sensitive	8
Tawny-edged skipper	*Polites themistocles*	habitat-sensitive	7
Gorgone checkerspot	*Chlosyne gorgone*	habitat-sensitive	5
Checkered white	*Pieris protodice*	disturbance-tolerant	2
Silver-spotted skipper	*Epargyreus clarus*	habitat-sensitive	2
American painted lady	*Vanessa virginiensis*	disturbance-tolerant	2
Dion skipper	*Euphys dione*	habitat-sensitive	1

[a]*Habitat categories are based on response to the high level of disturbance in Iowa. Those categorized as disturbance-tolerant do well in farms and cities; those categorized as habitat-sensitive are restricted to less-disturbed (though not necessarily native) habitat.*
[b]*Not native to the United States.*
[c]*Prairie specialist.*

ences in relative mortality based on plot type and road-surface type (paved or gravel). For the road-surface type we used only weedy roadsides because there was a relatively even number of paved and gravel roads (n = 13 and 16, respectively). Grassy roads were predominantly gravel and prairie roads were predominantly paved. In general, road surface can be a surrogate for traffic volume, gravel roads having low volume and paved roads having high volume. For the behavior study, we used logistic regression (PROC LOGISTIC; SAS Institute 1990) to determine the effect of plot and road-surface type on the probability that an individual approaching the road would cross.

Results

We identified a total of 3906 butterflies of 25 species during 953 surveys over the course of the summer (Table 1). There was no significant interaction of survey round with roadside type for any of the response variables examined; therefore, data from all rounds were combined for analysis.

More habitat-sensitive individuals were observed in prairie roadsides than in grassy and weedy roadsides (Fig. 2a), although only grassy and prairie roadsides were significantly different ($p < 0.02$). Disturbance-tolerant spe-

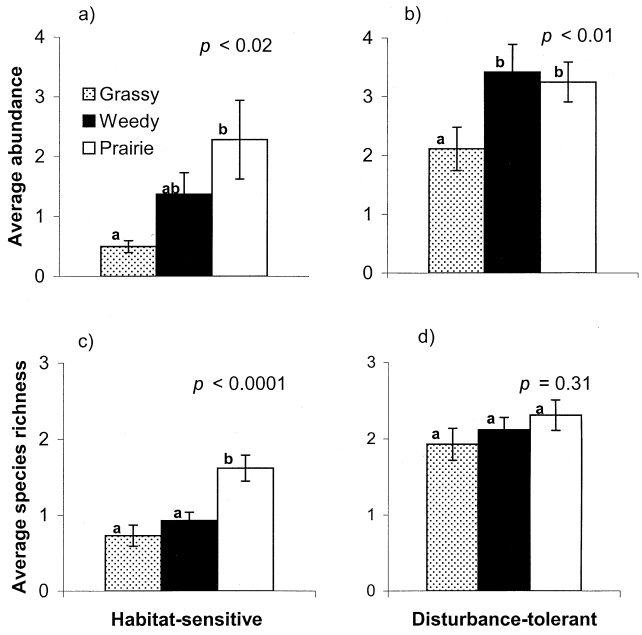

Figure 2. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies in grassy, weedy, and prairie roadsides in central Iowa. Values are based on an analysis of variance. Different letters indicate means that are significantly different.

cies had approximately two-thirds the number of individuals in grassy roadsides compared to weedy and prairie roadsides; there was no difference between weedy and prairie roadsides (Fig. 2b). There were about twice as many habitat-sensitive species in prairie roadsides than in grassy and weedy roadsides (Fig. 2c). Species richness of disturbance-tolerant species did not differ among the three roadside types (Fig. 2d).

There were no significant differences in species richness or overall abundance between restored and native prairie roadsides for both habitat-sensitive and disturbance-tolerant species (Table 2). Only richness of habitat-sensitive species showed a trend, with more species in native than weedy roadsides. Although this result was not significant ($p = 0.13$), there were only four native roadsides, so there was little statistical power to detect a difference. Neither richness nor abundance of habitat-sensitive species differed between prairie roadsides (native and restored combined) and nonroadside prairie remnants (Table 2). Disturbance-tolerant species had almost twice the abundance in roadsides than in prairie remnants (Table 2; $p < 0.05$) and a marginally higher richness in roadsides (Table 2; $p = 0.09$).

The number of species in flower explained little of the overall variation in butterfly numbers ($r^2 = 0.07$, $p < 0.0001$). There was a clear trend, however, of increase in mean butterfly richness and abundance as flower richness increased; this trend was observed within all three roadside types (Fig. 3). In contrast, percent cover of flowers showed no significant effect on either richness or abundance. There was a marginally significant increase in richness of habitat-sensitive species as restoration size increased (Fig. 4c, $p = 0.08$). Restoration size had no effect on disturbance-tolerant butterflies (Fig. 4b & 4d).

Mortality Study

The survey of road-killed butterflies showed that although the absolute number of butterflies found was lowest near grassy roadsides, the relative mortality rate along grassy roadsides may actually have been higher (Fig. 5a). In addition, relative mortality was about nine times higher on paved than on gravel roads (Fig. 5b). A significantly higher percentage of individuals crossed roads with grassy and weedy roadsides than those with prairie roadsides (49, 44, and 23% respectively, $p < 0.001$). There was no effect of road surface on road-crossing behavior. We observed 108 butterflies cross the road and only 3 were hit by a vehicle, for an overall mortality risk of 2.8%. Mortality risk was higher for paved than gravel roads (7% and 1%, respectively). The low number of individuals hit did not allow for a statistical analysis of mortality risk for any of the factors examined.

Discussion

Our results show that management of roadside vegetation has a profound effect on butterfly communities. The prevalence of grassy, weedy, and prairie roadsides is a direct result of the roadside management practices of each county within Iowa. Both habitat-sensitive and disturbance-tolerant species showed an increase in weedy and prairie roadsides that was not seen in grassy roadsides. Habitat-sensitive species showed a positive response to active prairie restoration, with higher overall abundance and species richness in prairie than in weedy roadsides, indicating that at least some individuals responded to restoration in roadsides. Disturbance-tolerant species showed increased abundance in response to IRVM techniques, but there was no increase associated with active prairie restoration.

Roadsides as Additional Habitat

Butterflies have complex life cycles and need different resources at each stage of development. For roadsides to truly add habitat for a particular species, the habitat must either provide resources necessary for all life stages or be within reasonable distance of required resources. In addition, increases in fecundity must outweigh possible increases in mortality. In other words, habitat should be able to support a population without depending on immigrants from other areas (Pulliam 1988). Under these criteria, it is difficult to rigorously measure the value of habitat to any particular species without collecting de-

Table 2. Comparison of the mean abundance and species richness of both habitat-sensitive and disturbance-tolerant butterflies in different types of prairie habitat in central Iowa.[a]

Dependent variable	*Habitat category*	*Roadside comparison*					*Prairie comparison*				
		restored	*native*	*df*	t	p > t	*roadside*	*remnant*	*df*	t	p > t
Abundance	habitat-sensitive	2.43 (0.99)	1.99 (0.39)	10	0.305	0.767	2.28 (0.66)	1.59 (0.17)	12.3	1.02	0.327
	disturbance-tolerant	3.24 (0.47)	3.26 (0.53)	10	0.033	0.975	3.25 (0.34)[b]	1.75 (0.51)[b]	14[b]	2.239[b]	0.042[b]
Species richness	habitat-sensitive	1.43 (0.18)	2.00 (0.33)	10	1.649	0.13	1.62 (0.17)	1.70 (0.12)	14	0.235	0.818
	disturbance-tolerant	2.16 (0.27)	2.60 (0.20)	10	1.039	0.323	2.31 (0.20)	1.61 (0.27)	14	1.828	0.089

[a]*Comparisons were made between restored and native prairie roadsides (roadside comparison) and between prairie roadsides and nonroadside prairie remnants (prairie comparison) with a t test. Standard errors are shown in parentheses after mean values.*
[b]*Significance at the 0.05 level.*

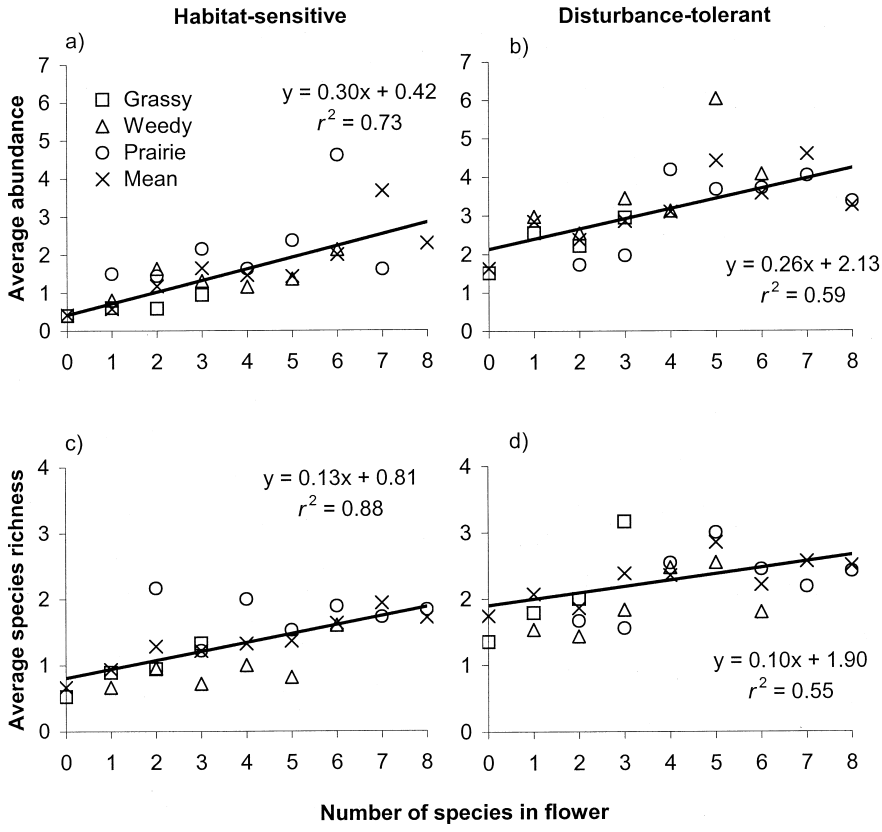

Figure 3. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies as the number of species in flower increased in roadside plots in central Iowa. Regressions were performed on mean values, but values for roadsides classified as grassy, weedy, and prairie are also illustrated.

mographic data (Van Horne 1983). The greater density and richness in both weedy and prairie roadsides, however, offers preliminary evidence that IRVM may add habitat for some butterfly species.

By increasing the diversity and amount of forbs in roadsides through direct planting and decreased use of herbicides, IRVM increases both the nectar and host-plant resources in the surrounding landscape for many species. The most common butterflies seen in our surveys (*Colias* sp. and *Everes comyntas*) both use a variety of legumes as host and nectar plants (Scott 1986). Legumes were dominant in weedy roadsides (by design) and often in prairie roadsides. Therefore, it is likely that both weedy and restored roadsides provide habitat for the most common butterflies in Iowa. Disturbance-tolerant butterflies, which are at little risk in Iowa, almost certainly benefit from IRVM practices, but they probably gain little, if anything, from actual prairie reconstruction. In contrast, habitat-sensitive species did respond to active prairie restoration over passive colonization of weeds. For some species, therefore, prairie restoration may be necessary to realize a benefit from IRVM.

Our data suggest that individual mortality risk is highest in grassy roadsides, despite the fact that most are located along gravel roads. This may be because individuals are more likely to exit grassy roadsides than prairie roadsides (49% and 23%, respectively). Being near a paved road greatly increased mortality risk, however, and most restoration projects are located along paved roads. The fact that mortality risk was lowest in prairie roadsides even though these areas tended to be paved may be explained by a reduced tendency of the butterflies to exit the roadside habitat. That overall abundance was higher in prairie roadsides may also indicate either that birth rates are offsetting mortality or that individuals are being drawn into the population from elsewhere. If the latter is the case, then roadsides attractive to butterflies may be acting as a high mortality trap.

Roadsides as Corridors or Stepping Stones between Habitat

Although we did not collect data specifically to test the hypothesis that roadsides can "connect" populations in fragmented habitat, our data offer some preliminary evidence that restored roadsides may be able to link habitat. The IRVM increases nectar resources in the landscape, which provides energy for an individual moving through the landscape searching for a new, suitable habitat patch. For species that can reproduce in roadside habitat, roadsides may function as stepping stones between reserves by decreasing the distance between habitat fragments. Even in situations where roadsides cannot sustain a population, limited reproduction in roadsides could add individuals to the migrant pool, effectively increasing linkage between isolated populations.

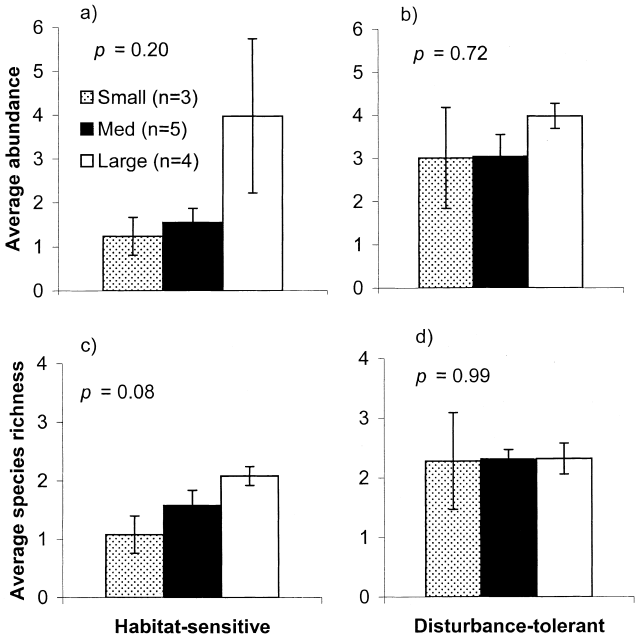

Figure 4. Average abundance of (a) habitat-sensitive and (b) disturbance-tolerant butterflies and species richness of (c) habitat-sensitive and (d) disturbance-tolerant butterflies based on length of roadside restoration in central Iowa. Restoration length was categorized as small (<800 m), medium (800–5000 m), and large (>5000 m). Values are based on an analysis of variance. Different letters indicate means that are significantly different.

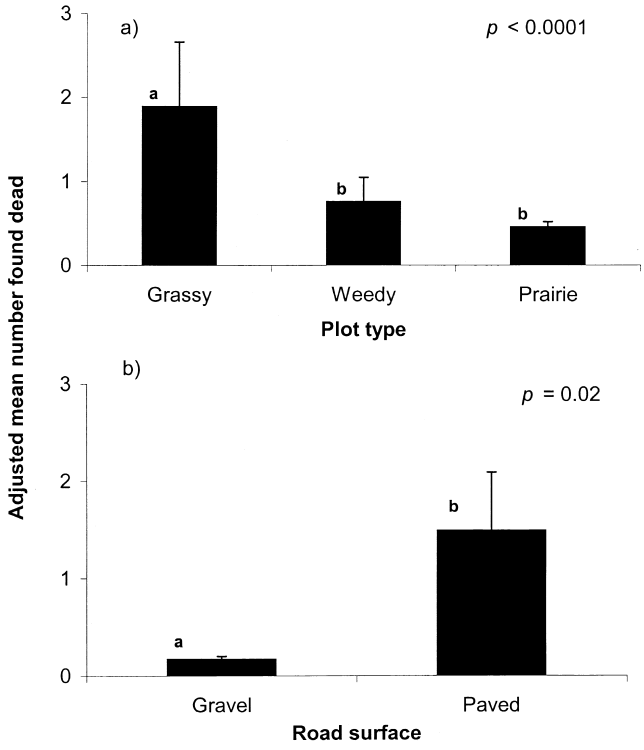

Figure 5. Number of individual butterflies found dead on the road divided by the number seen alive during roadside surveys in central Iowa, based on (a) roadside type and (b) road surface. Values are based on an analysis of variance. Different letters indicate means that are significantly different.

The most rigorous evidence supporting corridor value would be densities higher in connected than in unconnected patches (Beier & Noss 1998), but this type of data is rare (but see Haddad & Baum 1999). With few exceptions, restored roadsides do not exist as a continuous corridor between prairies or any other grassland reserve. At present, therefore, it is impossible to directly test the ability of roadsides to act as corridors between habitat fragments. In lieu of this evidence, two approaches have been taken to gather evidence that linear strips of habitat such as roadsides may function as corridors. The first and most common is to demonstrate that animal richness or density is higher in corridor than in noncorridor habitat, which we have demonstrated for habitat-sensitive species. The second type of data demonstrates that individuals tend to reflect off habitat boundaries, thus increasing the likelihood of moving down a corridor toward a connecting patch (Soulé & Gilpin 1991; Lima & Zollner 1996; Schultz 1998; Haddad 1999). We offer preliminary evidence for this by showing that individuals are most likely to turn at the boundary of prairie roadsides compared with grassy and weedy roadsides (77%, 51%, and 56% respectively).

This preliminary evidence suggests that butterflies may be able to use prairie roadsides as corridors or stepping stones. Butterflies unable to breed in weedy roadsides need to arrive at suitable habitat within their lifetime or the corridor acts as a sink rather than facilitating movement between patches. Even restored and native prairie roadsides may not be able to support populations of some butterfly species, and the only way these species could benefit would be if roadsides functioned to direct movement between habitat patches. As roadside restoration continues, we will be able to explore this issue more rigorously. One factor that needs to be considered is that as restored roadsides become more prevalent, prairie roadsides may become a continuous grid of linear habitat. If this occurs, roadsides may act as new habitat but may not have the ability to connect isolated patches because most roadside prairies will not lead anywhere. Thus, the question of whether reproduction can occur in roadsides will become even more critical.

Roadside Restoration versus Native Roadsides and Remnant Prairies

Richness of habitat-sensitive species was the only variable that showed a trend toward an increase in native com-

pared with restored roadsides (Table 2). Species richness is an important indicator of habitat quality, and our results indicate that native roadsides may be superior to restoration for some habitat-sensitive species. That it was not significant may be due to small sample sizes. But with only four native roadsides surveyed and a highly variable system, it is difficult to draw any strong conclusions. Given the rarity of native prairie remnants, however, preservation of these roadsides should be made a priority.

Our finding that habitat-sensitive species differed little in abundance between actual prairie remnants and prairie roadsides should be interpreted with caution. Butterfly communities vary a great deal among prairies (personal observation). We used only four prairie locations in this study, although they were among the highest-quality prairies in central Iowa. The largest, highest-quality site was mowed after the first round of surveys (data after mowing were not collected), which may have influenced the outcome of the results. Nevertheless, our results indicate that roadside butterfly communities appear similar in structure to a subset of central Iowa prairies. Once again, the lack of demographic data makes it difficult to compare the true value of either habitat type.

Conclusions

Integrated roadside vegetation management likely provides additional habitat for Iowa's most common disturbance-tolerant butterflies. These practices result in roadsides with more nectar sources and an increase in host plants for many of the most common species in Iowa. Yet these butterflies are in little danger, and focus should be placed on habitat-sensitive species. Our data indicate that roadside restoration may add habitat and has the potential to provide corridors for at least some habitat-sensitive species. Our results suggest that larger restoration efforts providing a greater richness of flower species will most benefit butterfly communities. Caution must be taken, however. Roadside restoration may be attracting habitat-sensitive species to areas where they have little hope of reproducing or may be doing little to direct species toward new habitat because no specific effort is being made to restore roadsides between prairie fragments. If roadside habitats do act as sinks for some species, as restoration continues and becomes more prevalent in the landscape, they have the potential to do more harm than good (Danielson 1992). Source-sink dynamics are notoriously difficult to demonstrate but must be understood before the real benefit of roadsides to butterfly communities can be assessed. Although we were not able to consider demographic information, our data indicate a positive effect of roadside restoration on Iowa's remaining sensitive species. As roadside restoration continues in Iowa and throughout the world, there is a need to rigorously assess the effects of restoration on habitat-sensitive species.

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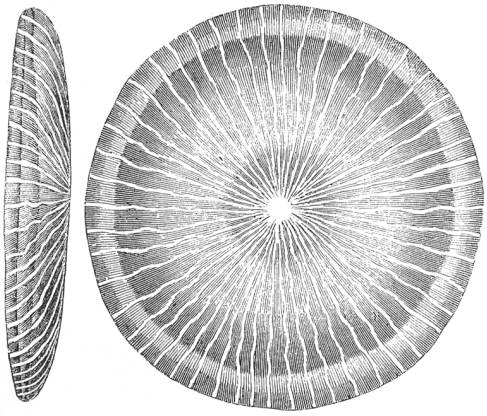

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Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa

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Summary

1. The behaviour of two butterfly species, a habitat specialist (*Speyeria idalia*) and a habitat generalist (*Danaus plexippus*), was tracked at four prairie edges to determine the extent to which edges act as a barrier to emigration. The four edge types studied were crop, road, field and treeline. The edges differed in structure ranging from high-contrast (treeline) to low-contrast (field).

2. *S. idalia*, the habitat specialist, responded strongly to all edges, even those with low structural contrast. However, *S. idalia*'s response was strongly affected by conspecific density at crop and field edges; individuals were less likely to exit from high density plots. *S. idalia* responded to edges both by turning to avoid crossing them, and returning to the plot if they had crossed.

3. *D. plexippus* responded strongly only to treeline edges. Wind direction and time of year were important factors influencing behaviour at edges for this species. Conspecific density was not a significant factor affecting their behaviour. *D. plexippus* responded to edges by not crossing them, but rarely returned once they had crossed.

4. In highly fragmented landscapes, such as the one in which this study occurred, butterflies which show little or no response to edges may exhibit high emigration rates because of the high probability of encountering an edge in small habitat patches. Butterflies may respond strongly to even subtle habitat boundaries, but those responses may be modified by the edge structure, local environment or other conditions. Therefore, modifying edge structure may be a way to influence emigration rates, making it a useful tool for conservation.

Key-words: edge permeability, habitat fragmentation, lepidoptera, tracking study.

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Introduction

The movement of individuals between subpopulations is a critical factor in the population dynamics of organisms with fragmented distributions (Levins 1969; Taylor *et al.* 1993; Ims & Yoccoz 1997). This issue has recently gained considerable practical importance because remaining natural habitat has become increasingly fragmented by human activity. Populations occupying these fragmented landscapes are generally assumed to be more isolated and vulnerable to the stochastic processes that may cause local extinctions (MacArthur & Wilson 1967). Movement between habitat patches can 'rescue' populations from local extinction (Brown & Kodric-Brown 1977) and reduce inbreeding depression (Spieth 1974). Despite the obvious importance of interpatch movement, we know very little about how readily most animals move through heterogeneous landscapes (Ims & Yoccoz 1997). One reason is the difficulty of gathering the field data necessary to estimate movement parameters and measuring rare, but important, long-distance migration events (Higgins & Richardson 1999).

One solution that has been used to gain insight into complex, difficult-to-measure processes is to break that process into parts and study each step separately. Our study focuses on the first step of interpatch movement: leaving a patch. Emigration rates are determined by the probability of occurrence of two events: (1) encountering the edge of a habitat patch and (2) crossing that edge once it is encountered (Stamps, Buechner & Krishnan 1987). Encountering an edge may be influenced both by the amount of edge relative to total patch area and the movement patterns of an individual within that patch. Although mobility clearly varies widely

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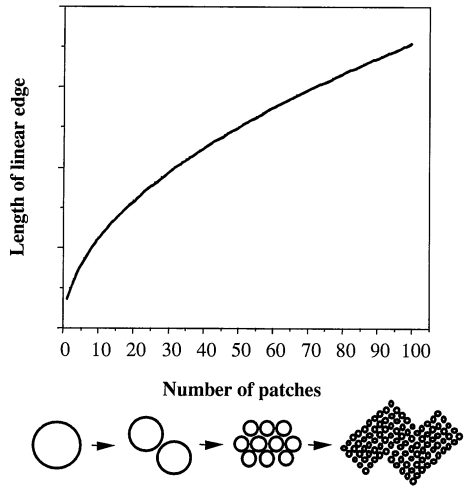

Fig. 1. Graphic representation of the increase in edge (measured as a two-dimensional attribute of a habitat patch) as a patch is divided into an increasing number of smaller, circular patches while holding area constant (reprinted, with permission, from Sisk & Margules 1993).

between species and even between individuals within a species, it is probably true for all species that, as the edge to interior ratio increases with increasing fragmentation (Fig. 1), the probability of encountering an edge will also increase.

The component of emigration that is much less easily understood and has not been widely studied is what occurs when an individual actually encounters an edge. There are several factors, both internal and external, that can influence whether or not an individual crosses an edge or remains within the habitat patch. Intrinsic factors may inhibit dispersal (Ehrlich 1961), and these factors may include genetic dispersal cues and an individual's expectation of fitness within the patch (for reviews of adaptive reasons for dispersal, see Johnson & Gaines 1990; Stenseth & Lidicker 1992). External factors, which have received much less study, include the structure of the edge (which includes abruptness and degree of contrast), the immediate local environment at the point of edge encounter, the quality of the habitat as a whole and the type and quality of the bordering habitat. Stamps *et al.* (1987) define the probability that an individual crosses an edge it has encountered as 'edge permeability'. However, individuals may not perceive an edge as a barrier to movement, or may not 'choose' to stay within a patch until they sample the habitat on the other side. Therefore, not only must the permeability of an edge be determined, but also the probability that an individual will continue on its path rather than return to the focal patch (thus becoming a true emigrant).

Few studies have examined specifically how animals respond when they encounter an edge, and most have focused on high contrast edges, such as a field bordered by a woodlot (see below). These studies have shown generally that individuals tend to avoid crossing into very different habitat types. Several tracking studies have shown that individuals are more likely to leave a patch through corridors of similar habitat (Johnsonn & Adkisson 1985; Sutcliffe & Thomas 1996; Machtans, Villard & Hannon 1997; Haddad 1999). However, all these studies used fields bordered by woodlands. Fry & Robson (1994) studied movement across less distinct boundaries and showed that butterflies were more likely to cross a field edge when the edge vegetation height was low. Thomas (1982) found a staryrid butterfly reluctant to cross from its breeding habitat in unimproved grassland into a bordering sown grass pasture. In a mark–release study, Kuussaari, Nieminen & Hanski (1996) found higher emigration rates from patches surrounded by more open habitat. Among these studies, there was little focus on how responses vary within and among species. Of the studies mentioned above, only Kuussaari *et al.* (1996) examined how emigration is influenced by other local factors and Haddad (1999) was the only investigator to collect data on more than one species. Identifying the factors that are most likely to influence the permeability of edges across a range of species and edge types is crucial in order to build a general framework of how edges affect populations.

In this study, we tracked the movement of two butterfly species with very different life-history characteristics at four prairie edge types in central Iowa. Individuals can respond to edges either by not crossing them (i.e. turning or stopping) or, having crossed into a new habitat type, individuals may reverse course and return to the patch. Variation in crossing and return behaviour can be used to determine which factors most influence edge response. Our objectives were to:

1. determine the edge permeability and return rates at four different prairie edge types;

2. measure how responses are affected by wind, conspecific density, flower abundance and time of year; and

3. compare the responses of two butterfly species with different habitat affinities.

STUDY SYSTEM: BUTTERFLIES IN PRAIRIES

Prairie is considered to be one of the most endangered ecosystems in the United States (Smith 1981). Tallgrass prairie is the most drastically affected with a decline in total area estimated between 82 and 99%, more than any other major ecosystem in North America (Samson & Knopf 1994). Iowa has been one of the most severely affected states, with less than 0·01% of the original tallgrass prairie remaining (Samson & Knopf 1994). Most prairie fragments in central Iowa are less than 4 ha and are often separated from the next closest prairie by several kilometres. A survey of 26 prairies in central Iowa showed that 50% of the total perimeter of prairie edges consisted of row crops and had a road or treeline as an intersecting boundary feature 38% of the time (Leslie Ries, unpublished data). Other common adjacent land types included old fields, pasture and woodland.

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Table 1. Description of each prairie used in the study and the number of individuals of each species tracked at each site

Prairie	Edge type (no. plots)	Size (ha)	Adjacent land	*D. plexippus* tracked	*S. idalia* tracked
Anders I[1,2]	Field (3)	8	Bromefield	52	12
Anders II[1,2]	Crop (3)	8	Soybeans	42	6
Doolittle	Treeline (3)	4	Corn	70	9
Harker	Treeline (2)	2	Corn	49	49
Kalsow	Road (3)	256	Corn	43	11
Kalsow	Crop (3)	256	Corn/Soy	59	51
Kish-Ke-Kosh	Field (2)	7	Lawn	24	0
Kurtz[2]	Road (3)	32	Corn	16	0
Liska-Stanek	Road (2)	16	Corn	19	64
Liska-Stanek	Crop (3)	16	Corn	16	83
Moeckley	Field (3)	16	Pasture	46	185

[1]Ander's property contains two 8-ha prairies.
[2]Reconstructed prairie.

The two butterfly species used in this study were chosen because they vary greatly in their life history characteristics and are sufficiently abundant to make rigorous comparisons of their behaviour. Regal fritillaries (*Speyeria idalia* Drury) are restricted to grasslands in the central and eastern United States and are declining throughout their range due to loss of habitat (Hammond & McCorkle 1983). In Iowa, *S. idalia* is generally restricted to native prairie where their host plants, prairie or bird's foot violet (*Viola pedatifida* Don and *V. pedata* L.), are found. A 1995 survey of 52 Iowa prairies revealed only 11 sites that had individuals present (Debinski & Kelly 1998). *S. idalia* is listed as a species of special concern in Iowa; however, Schlict & Orwig (1998) suggested that its status in Iowa be elevated to threatened. *S. idalia* is non-migratory and individuals generally stay within the same local area throughout their lifetime (Scott 1986; Nagel, Nightengale & Dankert 1991), although some adults have been known to move long distances (Opler & Wright 1999). The monarch (*Danaus plexippus* L.), on the other hand, is widespread in North America and found throughout much of the world (Scott 1986). Adults found in Iowa overwinter in Mexico and, over several generations, move north as far as southern Canada before returning to Mexico. Their host plants include several species of milkweed (Asclepiadaceae) which are found commonly in Iowa both in and outside of prairies.

Materials and methods

STUDY SITES

Based on the most common adjacent land and boundary characteristics of central Iowa prairies, four edge types were chosen for study: row crops with no intersecting boundary feature (CROP), row crops with a treeline between the crops and prairie (TREELINE), row crops with a gravel road between the crops and prairie (ROAD) and non-prairie grassland, such as old fields or pasture, with no intersecting boundary feature (FIELD). Native prairies in central Iowa were targeted for study, but two reconstructed prairies were included to increase the number of study sites. Our goal was to establish three plots each in three prairies for a total of nine study plots for each edge type. However, due to the limited number of larger prairie remnants in central Iowa, some sites contained only two plots. In addition, plots with treeline boundaries were established in only two prairies. Descriptions of each study site are in Table 1.

PLOT SET-UP AND SURVEY PROTOCOL

Plots were located inside prairies with one edge of the plot contiguous with the edge of the prairie (Fig. 2). Plots were placed randomly along the edge, subject to the restriction that they were at least 30 m from a corner and fully contained the appropriate edge type. Sites were eliminated if wetland habitat covered more than 25% of the area selected or if they were adjacent to another plot. Treeline plots were additionally restricted to contain no gaps in the treeline. Plots were 40 × 40 m and were marked using flags which were implanted in 1·2 m bamboo poles so they could be seen over the top of the vegetation. Flags were placed at 20 m intervals within the plot and they allowed butterfly positions to be approximated within one of the 16 10 × 10 m quadrats (Fig. 2).

All surveys were conducted between 1000 and 1900 h on sunny days. A survey was conducted by searching each of the 16 10 × 10 m quadrats within each plot for 2 min. Searches were suspended while tracking individuals and recording data. Quadrats were surveyed in random order, with a different set of random numbers chosen for each survey. Surveys were conducted until all 16 quadrats were completed or while weather and light conditions remained conducive to butterfly activity (i.e. sunny with low wind). Unfortunately, the sex of neither species could be identified consistently in flight, so no data on sex were collected. If an individual was spotted, it was tracked until it left the plot or remained perched for 5 min, at which time the track was abandoned. Individuals that left the plot were followed until they were at least 10 m beyond the plot. If they returned to the plot before exceeding

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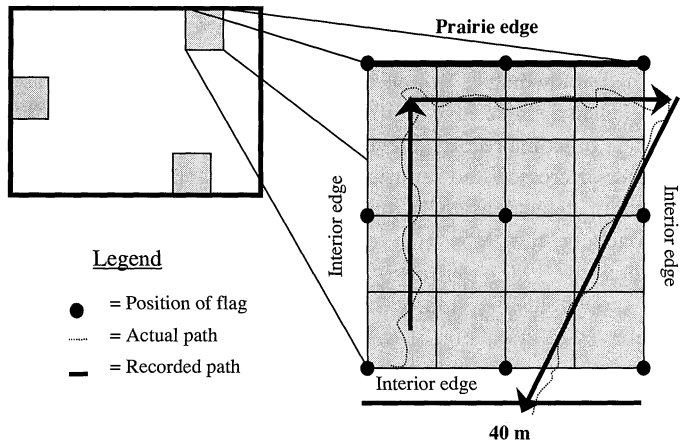

Fig. 2. Plot placement and survey design. Study plots were placed within prairies with one edge of the plot contiguous with the edge of the prairie. Each plot had 16 10 × 10 m quadrats. Butterfly positions within the plot were located using nine flags positioned at 20-m intervals. A representation of how an actual flight path would be recorded during a survey is shown.

the 10 m buffer, tracking continued. A 10-m buffer was used because there was often a barrier, such as a ditch or a barbed wire fence, separating the prairie from the adjoining habitats, so observations could only be made accurately for a short distance. An individual was considered to have exited the plot only when it left and did not return. Tracks were recorded so that small variations in flight direction were ignored (Fig. 2). Although this 'smoothing' of tracks was by necessity somewhat subjective, the subsequent analysis of movement was performed only on coarse-scale movements and therefore was not sensitive to the loss of this fine-scale information. Butterfly tracks were recorded for *S. idalia* and *D. plexippus*. All *S. idalia* present were tracked, but only the first 10 *D. plexippus* spotted in each survey were tracked. This approach was taken to avoid spending excessive amounts of time recording *D. plexippus* tracks because this species is often very abundant. Care was taken to avoid tracking the same individual twice during the survey, although there is no way to ensure this never happened. All plots were surveyed two or three times, with an average of 15 days separating surveys at the same plot to ensure a new group of individuals was being tracked.

In order to ascertain how movement was affected by local conditions, information on several factors was collected including wind direction, speed and flower abundance. To collect data on any one of these factors in great detail would have been prohibitively time-consuming. We therefore collected measurements that would allow us to look for coarse-scale effects, yet would not dominate our time spent in the field. Fluorescent flagging tape was attached to each pole in the survey plot, which allowed an estimation of the strength and direction of the wind to be recorded after each butterfly was tracked. This was accomplished by recording the approximate angle between the flagging tape and the pole as well as the direction the tape was blowing. In addition, a wind metre (Wind Wizard, model 281) was used to obtain average wind speeds for each survey day. Wind speed estimates were taken at breast height. For surveys where the wind ranged between 0 and 8 kph, the wind was classified as either still or low. On days when there was a consistent wind reaching 8–12 kph with gusts to 24 kph, wind was classified as low when the flagging tape was within 60° of the pole (approximately 2–8 kph based on comparisons with the wind speed indicator) or high when the flagging tape was greater than 60° from the pole (> 8 kph based on comparisons to the wind speed indicator). No surveys were carried out on days with average wind speeds greater than 12 kph because butterflies rarely flew under those conditions.

For each quadrat, an order of magnitude estimate was made of the total number of flowers in bloom. Using this information, each plot was categorized as having low, medium or high flower abundances which translated to an average quadrat abundance of approximately tens, hundreds or thousands of flowers, respectively. Eighty per cent of the flower surveys were conducted within 2 weeks of the butterfly survey and the remaining surveys were all completed within a month. At this scale of measurement flower abundance remained fairly constant from week to week, so the lag time in flower surveys would rarely have an impact on the flower abundance category that was assigned for each survey completed.

DATA ANALYSIS

Responses at the prairie edge were compared to responses at the three interior 'edges' of the plot (see Fig. 2). Because the three interior plot 'edges' were not true edges, they acted as a reference so that behaviour at the true edge could be compared to movements within the plot. Responses measured included which edge the individual used to exit the plot (exits were recorded when an individual crossed the edge and did not return), whether an individual on an intercept course with the edge crossed or avoided it (recorded

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separately at 0, 10, 20 and 30 m from the edge), and whether an individual that had crossed the edge returned immediately to the plot. Individuals that approached a single edge multiple times had only the ultimate outcome recorded (eventually crossed, never crossed, or crossed and returned). Edge permeability estimates, defined as the proportion of individuals approaching the edge that subsequently cross it (Stamps *et al.* 1987), were also calculated for each edge type. Individuals that approached within 10 m of the interior 'edges' (see Fig. 2) were used for these estimates so that the data were comparable to the estimates at the true prairie edge. Edge approaches were divided into 10 m sections at increasing distance from the edge.

A chi-square goodness-of-fit test was used to determine if individuals exited from the plot by crossing the prairie edge less frequently than expected if movements were random. Expectations of random frequencies for exit direction were based on the fact that each edge constituted 25% of the total perimeter of the plot. A chi-square test was also used to determine whether individuals avoided crossing prairie edges more frequently than the three interior 'edges' of the plot and at what distance from the edge responses were significantly different from behaviour at the interior 'edges'.

A stepwise logistic regression (SAS 1990) was used to model the influence of the edge (prairie vs. interior), edge type (crop, treeline, road, field), wind direction (with or against butterfly path), wind strength (low or high), conspecific density, flower abundance (low, medium, high) and week (1–10, modelled as a continuous variable) on the probability that an individual that approached an edge would (1) cross vs. not cross, and (2) return vs. not return (only if the individual had crossed). All factors, including interactions between density and each edge type as well as interactions between wind speed and direction, were entered into the logistic model. A significance level of 0·1 was used for both entry and retention in the model so any trends could be considered, even if they did not meet the standard 0·05 significance criteria. An index of density was estimated by calculating the mean number of individuals tracked during each of the 16 2-min surveys. In the event that tracking *D. plexippus* was cut off after 10 individuals (this occurred in 19 of 68 surveys), the density value was an underestimate. Density indices calculated applied only to each individual plot and not to the prairie as a whole.

For the purposes of logistic regression, no distinction was made between the three interior edges. However, a single butterfly may have approached each of the plot's four edges several times during the course of a single survey. In order to ensure the independence of points used in the logistic regression, only the response to the first edge each butterfly approached was used in the analysis. While this 'first approach' method allowed a rigorous comparison between behaviour at the true prairie edge with the interior 'edges', nearly one-third of the approaches towards the actual prairie edge were dropped from the analysis. Because behaviour at the prairie edge was the focus of our study a second, similar analysis was performed exclusively on the approaches towards the prairie edge. This second 'prairie edge' analysis allowed all data on behaviour at the true prairie edge to be retained.

Results

A total of 72 surveys where either *S. idalia* or *D. plexippus* were recorded were completed between June 21 and August 31, 1997. Table 1 shows the number of individuals of each species tracked at each prairie. A total of 470 *S. idalia* were tracked during 43 surveys; 436 *D. plexippus* were tracked during 68 surveys.

EXIT DIRECTION

Of the 433 *S. idalia* that were tracked until they left the plot, only 42 individuals exited by crossing the prairie edge. A chi-square goodness-of-fit test showed that exit directions differed significantly from random at treeline, crop and field edges with a strong bias towards individuals remaining in the prairie (Fig. 3a). The strongest response was seen at the treeline edge where only 4% of individuals exited the plot by crossing the prairie edge ($\chi^2 = 12{\cdot}41$, d.f. = 3, $P < 0{\cdot}001$). Exits at road edges did not differ significantly from random ($\chi^2 = 0{\cdot}667$, d.f. = 3, $P = 0{\cdot}95$). Of 412 *D. plexippus* tracked, 85 exited the plot by crossing the prairie edge. Exit directions differed significantly from random only at the treeline edge ($\chi^2 = 13{\cdot}13$, d.f. = 3, $P < 0{\cdot}001$; Fig. 3b).

EDGE PERMEABILITY AND DISTANCE OF RESPONSE (TURNING BEHAVIOUR)

Boundaries were less permeable to *S. idalia* than to *D. plexippus* (Table 2). Both species had the lowest permeability estimates at treeline edges, although the estimate was about three times higher for *D. plexippus* compared to *S. idalia*. *S. idalia* showed a stronger response at crop and field edges compared to road edges. *D. plexippus* showed similar responses at road, field and crop edge types. These estimates were only slightly lower than the estimate at the interior 'edges', which are used as a reference to compare responses at true edges to movements within the prairie. Interior 'edges' had the highest permeability estimates and were similar for both species (Table 2).

Figure 4 shows the proportion of individuals that avoided crossing each edge type as distance from the edge increased. Individuals that did not turn at 0 m subsequently crossed the edge. At all four edge types, *S. idalia* avoided crossing the edge more frequently compared to the interior edges between 0 and 9 m from the edge ($P < 0{\cdot}001$) and 10–19 m from the edge ($P < 0{\cdot}001$). After 20 m, however, no significant differences were found in turning frequencies among the five edge types. *D. plexippus* turned more frequently within

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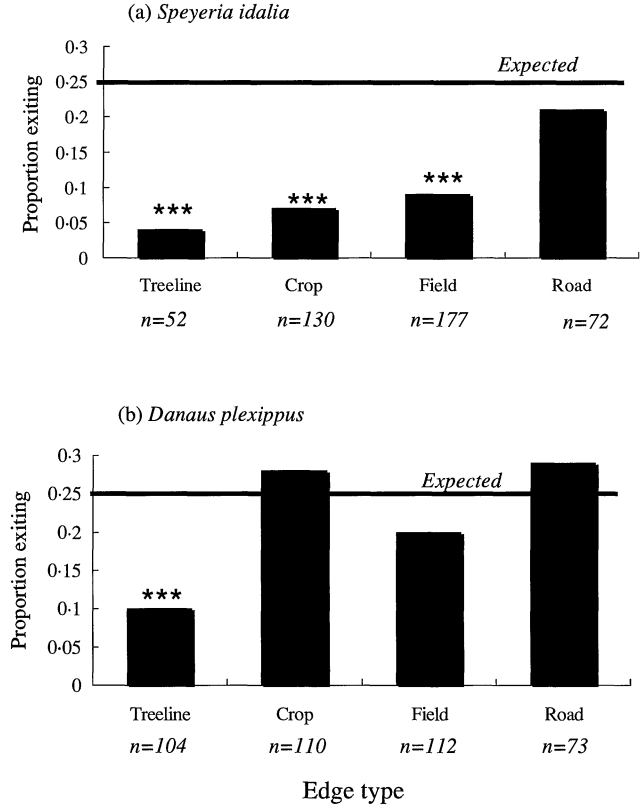

Fig. 3. Proportion of *S. idalia* (a) and *D. plexippus* (b) leaving the plot by crossing the prairie edge. Values less than 25% indicate a bias against crossing the edge because the prairie edge constitutes 25% of the perimeter of the plot. Differences between expected and observed values were tested using a chi-square goodness-of-fit test (***$P < 0{\cdot}001$).

Table 2. Estimates of edge permeability for *S. idalia* and *D. plexippus* for each edge type including interior edges. Edge permeability is defined by Stamps *et al.* (1987) to be the proportion of individuals approaching an edge that cross. The 95% confidence interval range (one-sided) is indicated in parentheses

Edge type	*Speyeria idalia*	*Danaus plexippus*
Treeline	0·08 (0·10)	0·24 (0·13)
Crop	0·29 (0·11)	0·64 (0·13)
Field	0·25 (0·09)	0·50 (0·14)
Road	0·43 (0·15)	0·68 (0·16)
Interior	0·70 (0·05)	0·75 (0·05)

10 m from the edge ($P < 0{\cdot}001$) at only the treeline edges. The 20–29 m distance also showed a significant difference between edge types ($P < 0{\cdot}05$); however, this result should be interpreted with caution due to the fact that this response class had a small sample size resulting in expected values less than five.

RETURN BEHAVIOUR

S. idalia that crossed the prairie edge returned more frequently than those that crossed the interior 'edges', and the strongest responses occurred at the crop and field edges (Fig. 5a). *D. plexippus* uniformly showed a low return rate; less than 10% of the individuals returned to the prairie after crossing the edge at all edge types (Fig. 5b). For both *S. idalia* and *D. plexippus*, only about 2% of the individuals who crossed the interior edges returned to the plot. Treeline edges were excluded from this analysis because individuals that crossed the treeline could no longer be seen. Due to the extremely low number of individuals that returned after crossing the edge, the expected number of individuals returning to the plot was less than one. Therefore, chi-square analyses were not possible.

LOGISTIC REGRESSION – *S. IDALIA*

For *S. idalia*, the factors of week and edge type were strongly correlated. This was not due to allocation of effort, but to pulses in butterfly abundances in certain prairies. For that reason, week was excluded as a factor from this analysis. *S. idalia* has no known trends in seasonal movements (Scott 1986) and no trend in movement with respect to week was evident in our data, so it is unlikely that including week is critical for this analysis. *S. idalia* was found only in prairies where flower abundances were generally high; of all the surveys, only two plots out of 43 were categorized as low. Therefore, low and medium flower categories were combined and flower abundances were scored as either medium or high. One survey that had a markedly higher proportion of individuals crossing the edge compared to other surveys with similar conspecific densities was identified as an outlier (circled in Fig. 6b,c) and excluded from

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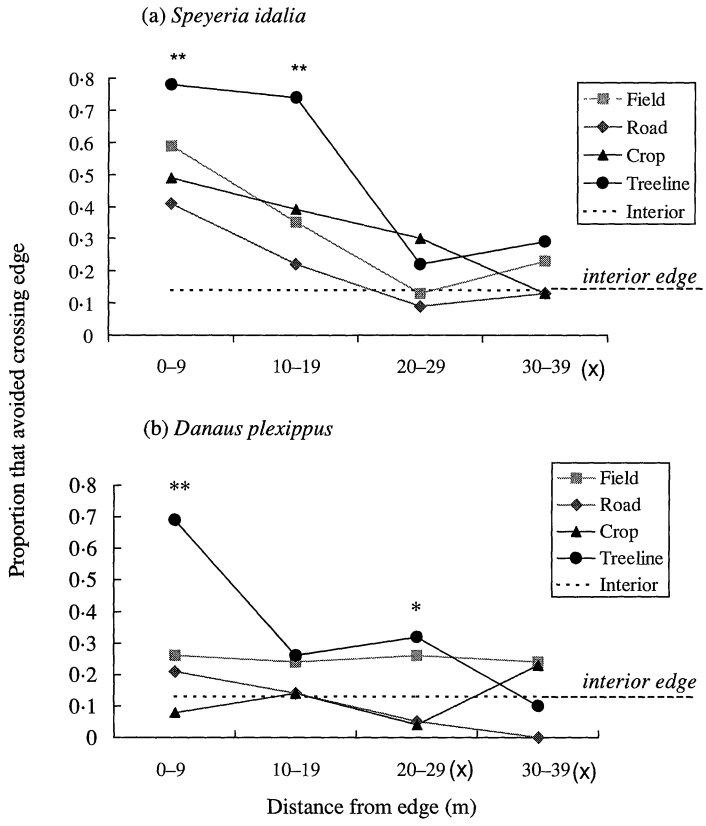

Fig. 4. Proportion of *S. idalia* (a) and *D. plexippus* (b) turning to avoid crossing the edge as distance from the edge increases. The proportion of individuals that turned to avoid crossing the interior edges is also shown. Each distance category was tested for differences in proportion avoiding crossing the edge between edge types using a chi-square goodness-of-fit test (**$P < 0{\cdot}001$,*$P < 0{\cdot}05$). Distances with low expected values are marked with an (x) and therefore the significance test should be interpreted with caution.

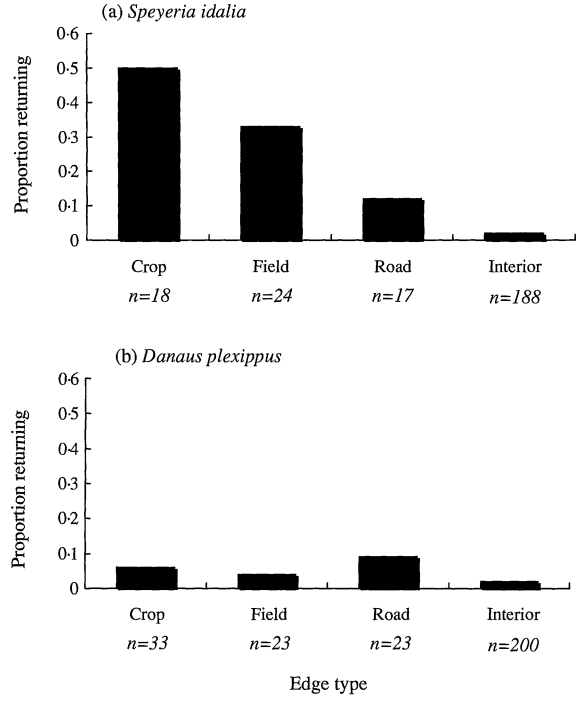

Fig. 5. Proportion of *S. idalia* (a) and *D. plexippus* (b) that returned to the plot after crossing the prairie edge. The treeline edge type was excluded because, once individuals crossed the edge, they could no longer be seen.

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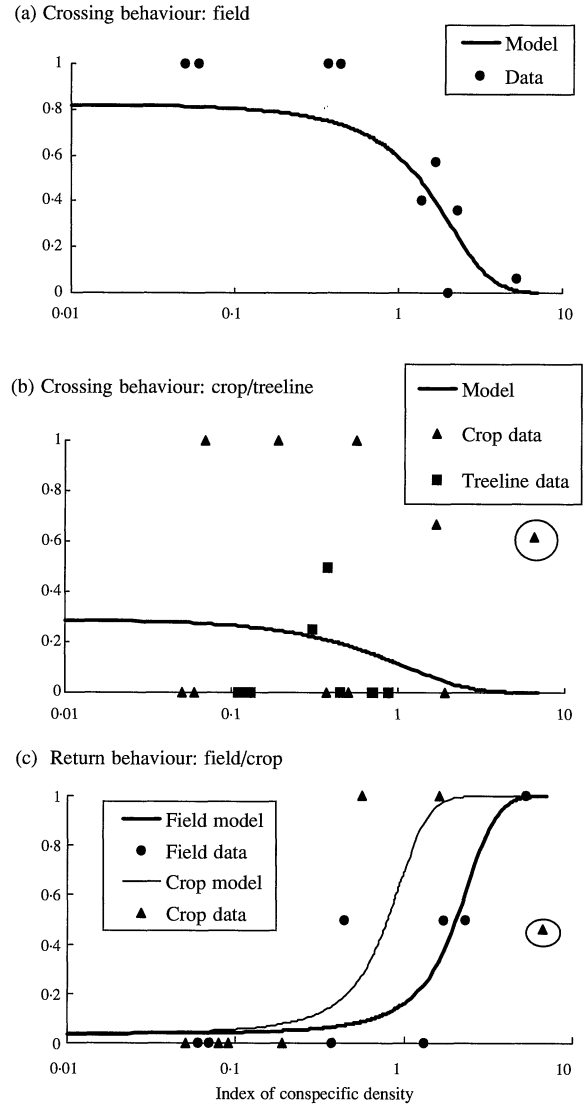

Fig. 6. For *S. idalia*, the probability that an individual approaching a field edge (a) or a crop or treeline edge (b) will cross the edge, and the probability that an individual who has crossed a field or crop edge will return to the plot (c) as conspecific density increases. Density values are based on the number of individuals observed in a two minute period. Lines represent estimated probabilities based on parameters generated by a logistic model (Tables 3 and 4). Points represent the observed proportion of individuals crossing the prairie edge during one survey. Results are shown for an analysis performed only on behaviour at true prairie edges. An outlier excluded from the analysis is circled (b,c).

the logistic regression. This point represents the only survey completed during the entire summer where there were high, sustained winds (up to 15 kph) blowing directly towards the prairie edge. However, it should be noted that even during that survey, only seven of 50 (14%) individuals tracked exited the plot by crossing the prairie edge. When this outlier was included in the analysis, similar results were obtained, but crop edges did not show a density effect. The parameter estimates of factors selected by the stepwise process are summarized in Tables 3 and 4 and Fig. 6.

S. idalia was less likely to cross prairie edges as compared to interior 'edges', especially as conspecific density increased (Table 3). This pattern was strongest at field edges (Fig. 6a) and weaker at crop and treeline edges where the overall probability of crossing was much lower (Fig. 6b). It is important to note that density values varied widely *within* some prairies and the response to conspecific density was seen within these prairies. Results from the two analyses ('first approach' and 'prairie edge') were similar, except for at road edges which showed an opposite trend under the two different analyses (Table 3). This result may be due to the fact that there were no surveys done at road sites with high densities comparable to the other three edge types. The highest density value for road plots was 1·3 individuals seen every 2 min, whereas the highest values for field and crop plots where 5·3 and 6·6, respectively. Wind was a factor only in the model that included interior edges and flower abundance was never included in the model (Table 3). The analysis including all prairie edge approaches showed that the probability of return increased with increasing conspecific density ($P < 0{\cdot}01$) and was higher at crop edges than at other kinds of

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Table 3. Factors selected by the stepwise logistic procedure as affecting crossing behaviour for *Speyeria idalia* and *Danaus plexippus*. Results are shown for (1) an analysis where the first edge approached was used, and (2) when only approaches towards the prairie edge were included. Standard errors are in parentheses; d.f. = 1 for all parameter estimates. Significance level required for entry and retention in the model was 0·1. Edge interactions signify this factor was only significant when an individual was approaching the prairie edge as opposed to an interior edge. Graphical representations of major results are shown in Fig. 7 (*$P < 0·10$, **$P < 0·05$, ***$P < 0·001$)

	Speyeria idalia		*Danaus plexippus*	
Factors chosen	First approach parameter (SE)	Prairie edge parameter (SE)	First approach parameter (SE)	Prairie edge parameter (SE)
Intercept	0·21 (0·16)	−0·90 (0·36)**	0·61 (0·42)	−1·71 (0·68)**
Prairie edge	NS	–	NS	–
Density (at prairie and interior edges)	−0·13 (0·06)**	–	NS	–
Density × prairie edge	−0·83 (0·23)***	−1·15 (0·28)***	NS	NS
Density × road edge	−3·04 (1·17)**	1·74 (0·50)***	NS	NS
Density × crop edge	−1·28 (0·41)*	NS	NS	NS
Field edge	0·90 (0·55)*	2·43 (0·56)***	NS	NS
Treeline edge	−2·44 (1·05)**	NS	−2·44 (0·77)**	−0·94 (0·45)**
Wind blowing towards approach edge	0·49 (0·22)**	NS	1·01 (0·23)***	0·74 (0·38)
Week†	–	–	NS	0·29 (0·10)**
Flower abundance‡	NS	NS	−0·29 (0·17)*	NS
Concordance	65·7%	78·0%	52·7%	70·0%
Pearson goodness-of-fit	$P = 0·0001$ (d.f. = 90)	$P = 0·001$(d.f. = 43)	$P = 0·34$ (d.f. = 140)	$P = 0·28$ (d.f. = 66)

†Week values range from 1 to 10.
‡Flower abundance values are 1 (low), 2 (med), 3 (hi).
–Not included in regression model.

Table 4. Factors selected by the stepwise logistic procedure as affecting return behaviour for *Speyeria idalia*. Results are shown for (1) an analysis where the first edge crossed was used and (2) when only returns after crossing the prairie edge were included. Standard errors are in parentheses; d.f. = 1 for all parameter estimates. Significance level required for entry and retention was 0·1. Edge notations signify this factor was only significant when an individual was approaching the prairie edge as opposed to an interior edge. Graphical representations of major results are shown in Fig. 7 (*$P < 0·05$, **$P < 0·01$, ***$P < 0·001$)

	Speyeria idalia	
Factors chosen	All edges parameter (SE)	Prairie edge parameter (SE)
Intercept	−2·56 (0·21)***	−3·27 (0·98)**
Density (at prairie edge)	NS	1·61 (0·62)**
Crop edge	NS	2·50 (1·23)*
Concordance	Not calculated[1]	79·3%
Pearson goodness-of-fit	$P = 0·01$ (d.f. = 83)	$P = 0·39$ (d.f. = 16)

[1]Due to the fact that no factors were significant.

edges at lower butterfly densities ($P < 0·05$; Table 4, Fig. 6c).

LOGISTIC REGRESSION: *D. PLEXIPPUS*

D. plexippus only avoided crossing treeline edges ($P < 0·001$; Table 3, Fig. 7). When all edges were considered, higher flower abundances decreased crossing ($P < 0·05$); however, when only approaches toward the prairie edge were analysed, flower abundance dropped out of the model, and week became a significant factor ($P < 0·01$) with the probability of crossing increasing as the summer progressed (Fig. 7). Both analysis methods showed that wind blowing towards the edge of approach increased crossing (Table 3, Fig. 7). An analysis of return behaviour was not possible because too few individuals returned to the plot (Fig. 5).

Discussion

Our results show that habitat edges can act as a barrier to movement, even when the adjacent habitats are structurally similar. However, other environmental factors played a dominant role in modifying edge response. *S. idalia* responded strongly to field edges, but only when conspecific densities were high (Fig. 6a,c). Surprisingly, at high densities, the response of *S. idalia* to field edges, structurally a very subtle edge, was comparable to treeline edges, an extremely high contrast edge type (Fig. 6a,b).

We have also demonstrated that, along with the probability of crossing an edge, return behaviour is an important factor that should be considered when measuring responses to edges. For *S. idalia*, the combination of both avoiding crossing an edge (Fig. 4a)

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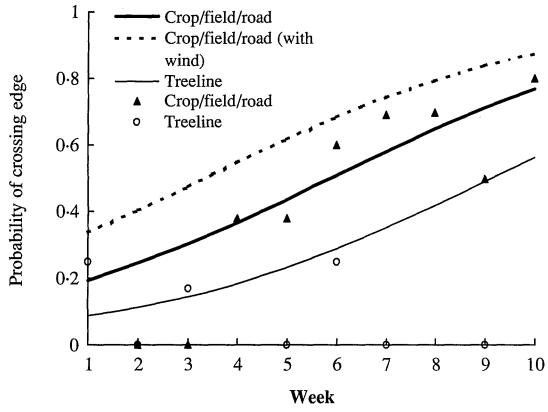

Fig. 7. For *Danaus plexippus*, the probability that an individual will cross the prairie edge as summer progresses. Lines represent estimated probabilities based on parameters generated by a logistic model (Table 3). Points represent the observed proportion of individuals crossing the edge during each week. The increased probability of crossing when wind is blowing towards the prairie edge is shown for crop, field and road edges, although the same increase is estimated for treeline edges.

and returning to the plot after crossing (Fig. 5a) was responsible for the overall pattern in exit direction observed (Fig. 3a). In contrast, the pattern of exit direction for *D. plexippus* (Fig. 3b) was caused solely by avoiding crossing an edge (Fig. 4b) rather than returning to the plot after crossing (Fig. 5b). This indicates that *S. idalia* may be responding to the quality of bordering habitat, whereas *D. plexippus* does not. Butterflies have been shown to return to patches from a distance of 100 m (Conradt *et al.* 2000); therefore, we probably underestimated the number of butterflies which returned to the prairie after crossing. However, the differences observed in return behaviour likely reflect the general tendency of each species to return to the patch.

With the exception of *S. idalia* at treeline edges, all permeability estimates were above 0·10, and ranged from 0·24 to 0·68 at the prairie edge (Table 2). According to Stamps *et al.* (1987), when permeability estimates are greater than 0·10 the size and shape of the patch are the most important factors determining emigration rates. Therefore, in this system emigration rates are most influenced by the probability of encountering an edge, which is likely to be high considering that most prairies are small (ranging from 1 to 10 ha). In Iowa therefore emigration rates are likely to be high. Although increased movement between habitat patches is considered to mitigate many of the problems associated with isolation (Brown & Kodric-Brown 1977), in the severely fragmented Iowa landscape increased dispersal may have an overall negative effect resulting from a drain on the local population (Thomas *et al.* 1998; Thomas & Hanski 1999) and a very low probability of finding a new patch. Therefore, modifying edge structure to reduce dispersal may become an important management option.

Our results demonstrate that two species with different life history characteristics responded to very different factors. *S. idalia* showed a stronger overall response to edges than *D. plexippus*, which may not be surprising considering the host plant of *S. idalia* is restricted to prairies and *D. plexippus* is a long-distance migrant. However, the results of this study cannot be used to make generalizations regarding the response of habitat specialists to edges because data on only one habitat specialist were collected. One reason *S. idalia* was chosen for study was because, despite its regional rarity, it is often locally abundant. There are several other prairie specialist butterflies resident in Iowa (Schlict & Orwig 1998), yet most of these species are found only in low densities, if at all. It may be that most prairie butterflies *do not* respond strongly to edges, and therefore consistently have low or zero densities in small prairie remnants while *S. idalia*, having a strong edge response, often maintains high densities where it occurs. To test this idea, surveys are necessary in much larger prairies where several prairie specialists persist.

S. idalia showed significant responses only within 20 m of the edge (Fig. 4a), *D. plexippus* within 10 m of the edge (Fig. 4b). This is consistent with the results of a tracking study done in South Carolina that showed three species of butterflies responded to a wooded edge only when within 16 m (Haddad 1999) and may reflect a general response range for butterflies. This range of response may also be an indicator of the extent to which 'edge effect' extends into a habitat, providing one method of estimating 'core' habitat area (Laurence & Yensen 1991).

RESPONSE OF *S. IDALIA* TO CONSPECIFIC DENSITY

S. idalia formed high-density aggregations within prairies. Individuals within these aggregations were less likely to cross the edge and were more likely to return to the prairie if they did cross compared to individuals outside of aggregations (Fig. 6). Many other insect species have been shown to form such aggregations (Turchin 1989) including aphids, beetles and caterpillar, as well as several species of butterflies. Reduction of migration from high density aggregations has also been noted for other species of butterfly (Brussard, Ehrlich & Singer 1974; Kuussaari *et al.* 1998).

The effect of density on emigration rate has important implications for conservation. If *S. idalia* are more likely to emigrate from low-density patches, population growth rates may decline with declining population levels, an example of the 'Allee effect' (Allee 1931). If this is the case, stochastic events causing populations to decrease may be exacerbated by higher emigration rates. In addition, re-establishing a population after extinction may also be less likely because initial population levels are likely to be low. Although higher emigration rates at lower densities have been documented in other butterfly populations (Gilbert & Singer 1973;

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Brussard *et al.* 1974; Brown & Ehrlich 1980; Kuussaari *et al.* 1998), our results show that this phenomenon also occurs *within* a single patch where there is variation in densities within that patch.

The density effect on edge response may also have implications for corridor use. In this system, roadside prairies have often been suggested as possible corridors between prairie remnants (Ries, Debinski & Wieland 2001). Corridors of habitat between patches have been proposed to reduce isolation in fragmented systems, but have remained controversial due to a lack of empirical evidence supporting their use (Rosenberg, Noon & Meslow 1997). If data on corridor use are lacking, edge reflectance has been suggested to be a predictor for targeting species likely to respond to corridors as a management tool (Soulé & Gilpin 1991; Schultz 1998; Haddad 1999). By those criteria, our results superficially indicate that *S. idalia* would be an ideal candidate for this type of management; overall, we found a strong reflective bias at edges (Fig. 4a). However, the fact that at low densities individuals showed a reduced response to edges may mean that *S. idalia* movement may *not* be directed by corridors because densities in corridors are likely to be low. However, managers could take advantage of the fact that certain edge types, such as treelines, tend to elicit a stronger response.

S. idalia did not appear to respond to road edges as barriers to movement (Fig. 4a), and the logistic regression showed mixed results to increases in density (Table 3). However, this may be explained by the fact that no plots near roads exhibited high densities relative to other edge types. The fact that surveys performed at road edges had relatively low densities may in itself explain the lack of response to road edges (Fig. 3a). Alternatively, individuals may be responding to some unknown factor in the local environment near roads, such as differences in temperature or the reflective nature of roads. Further study is necessary to establish if *S. idalia* truly has a differing response to road edges or if this was a spurious result.

THE INFLUENCE OF THE LOCAL ENVIRONMENT ON EDGE CROSSING AND RETURNS

Wind influenced the movement of *D. plexippus* much more so than *S. idalia*. In general, however, we avoided doing surveys on excessively windy days, and it was clear from observations that at higher wind speeds (above 10 kph), butterfly movement was affected to some degree. However, as wind increased *S. idalia* activity decreased, suggesting that individuals often dealt with wind by not flying. Therefore, it seems unlikely that wind exerts an important influence on *S. idalia* emigration rates. Wind exerted a much greater influence on the movement direction of *D. plexippus*; individuals were more likely to cross any edge of the plot (prairie or interior) when the wind was blowing towards it (Fig. 7). However, this may be indicative of the weak response of *D. plexippus* to prairie edges rather than a lesser ability of *D. plexippus* to control their flight direction with respect to the wind.

In this study, we used flower abundance as a surrogate for nectar abundance. High flower abundance decreased the probability that *D. plexippus* would cross all edge types when data using 'first approaches' were used (Table 3). However, flower abundance dropped out of the model when only behaviour at the true prairie edge was considered. This may be due to individuals turning more frequently within prairies (thus flying along a more convoluted path), without affecting responses to the true prairie edge. *S. idalia* did not show a significant response to flower abundance (Tables 3, 4). However, this result should not be used to draw general conclusions regarding the sensitivity of *S. idalia* to flower abundance. In this study, *S. idalia* were only found in the highest quality prairies where flower abundances were generally high. Nectar therefore may not have been a limiting resource for *S. idalia* in this case. In addition, coarse scale measurements of flower abundance may be a poor surrogate for nectar availability (Schultz & Dlugosch 1999).

D. plexippus were more likely to cross plot edges (prairie edges as well as interior) towards the end of the summer (Fig. 7), which coincides with their southward fall migration (Scott 1986). Haddad (1997) showed that during migratory periods, some butterflies are less likely to be deflected from their path, and this may have occurred in this case.

Conclusions

In contrast to earlier studies (Fry & Robson 1994; Kuussaari *et al.* 1996), we found that individuals can show strong responses to even subtle differences in vegetation structure. However, our results indicate that the responses of butterflies to prairie edges are highly variable, and dependent on the species, edge characteristics and the local environment experienced by an individual. Our results indicated that edge permeability may be the most important factor determining emigration rates in central Iowa, due to high edge permeability rates and the small size of individual prairies found there. However, the factors that influenced edge permeability were very different for *S. idalia* and *D. plexippus*, as was the range of their responses. The extent of this variability suggests that when estimating movement parameters, species specific responses and the influence of local conditions should be considered. It is clear from our results that in order to build a general framework of how landscape affects movement, responses of several species in a variety of environments needs to be measured. Even though our study only measured very small-scale movements, we suggest that edge structure can have important implications for population dynamics through its impact on emigration rates.

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POPULATION ECOLOGY - ORIGINAL PAPER

Butterfly edge effects are predicted by a simple model in a complex landscape

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Abstract Edge responses have been studied for decades and form a critical component of our understanding of how organisms respond to landscape structure and habitat fragmentation. Until recently, however, the lack of a general, conceptual framework has made it difficult to make sense of the patterns and variability reported in the edge literature. We present a test of an edge effects model which predicts that organisms should avoid edges with less-preferred habitat, show increased abundance near edges with preferred habitat or habitat containing complementary resources, and show no response to edges with similar-quality habitat that offers only supplementary resources. We tested the predictions of this model against observations of the edge responses of 15 butterfly species at 12 different edge types within a complex, desert riparian landscape. Observations matched model predictions more than would be expected by chance for the 211 species/edge combinations tested over 3 years of study. In cases where positive or negative edge responses were predicted, observed responses matched those predictions 70% of the time. While the model tends to underpredict neutral results, it was rare that an observed edge response contradicted that predicted by the model. This study also supported the two primary ecological mechanisms underlying the model, although not equally. We detected a positive relationship between habitat preferences and the slope of the observed edge response, suggesting that this basic life history trait underlies edge effects and influences their magnitude. Empirical evidence also suggested the presence of complementary resources underlies positive edge responses, but only when completely confined to the adjacent habitat. This multi-species test of a general edge effects model at multiple edge types shows that resource-based mechanisms can explain many edge responses and that a modest knowledge of life history attributes and resource availability is sufficient for predicting and understanding many edge responses in complex landscapes.

Keywords Ecotone · Ecological boundary · Fragmentation · Habitat edge · Predictive model

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Introduction

Understanding ecological responses to the presence of habitat edges is critical to understanding landscape-scale phenomena, such as the effects of habitat heterogeneity within a landscape mosaic and the impacts of habitat fragmentation (Murcia 1995). Edge effects have been studied for many decades (Lay 1938), with a tremendous number of

published studies emerging in the last 30 years, all confirming that many taxa respond behaviorally and numerically to the presence of habitat edges (for reviews, see Murcia 1995; Risser 1995; Lidicker 1999; Lahti 2001; Chalfoun et al. 2002; Sisk and Battin 2002; Ries et al. 2004). Edge responses have been shown to be far more common than responses to changes in habitat area per se; in fact, most patterns identified initially as area responses are probably scaled-up edge responses (Fletcher et al. 2007). Furthermore, incorporating knowledge of edge responses has improved predictions of species' distributions in fragmented landscapes (Temple 1986; Sisk et al. 1997; Ries 2003; Brand et al. 2006). Despite the importance of this topic, there has been no overarching theoretical framework (Murcia 1995; Cadnasso et al. 2003) or, until recently (Ries and Sisk 2004), a general model available to predict the responses of organisms to a variety of edge types.

This lack of a theoretical framework has made it difficult to make sense of the varied results reported in the edge literature. A specific example of this can be found in the limited literature on butterfly edge responses. Studies have shown that certain butterfly species either avoid (Schultz 1998; Haddad and Baum 1999) or are attracted (Ravenscroft 1994; Bergman 1999; Wahlberg 2001; Ide 2002) to certain edges. Although some of these studies include data showing how changes in microclimate or host plant distribution were associated with these patterns, there is no overarching framework to explain when specific butterfly species should be expected to avoid, be attracted to, or ignore specific edge types. Therefore, it is difficult to extrapolate these results to other species or landscapes or to develop a general understanding of which factors are most important in driving butterfly edge responses.

Focusing on the variability of edge responses may leave the impression that, despite decades of study, edge responses are so species and context specific that they constitute an idiosyncratic phenomenon that cannot be generalized. In contrast, in 2004 we proposed a general model of edge effects based on habitat associations and resource distribution (Fig. 1, Ries and Sisk 2004). Drawing on dozens of published studies on diverse species in a variety of landscapes, the model was able to correctly predict the direction of observed edge responses 83% of the time for birds (Ries and Sisk 2004), 91% of the time for plants, and 83% of the time for mammals (Ries et al. 2004).

The goal of the study reported here was to determine how well this model explains the great variability in edge responses observed for a suite of butterfly species in a complex riparian landscape characterized by several distinct edge types. To provide the first robust test of this model for an invertebrate taxon, we collected one of the largest datasets on butterfly edge effects and the first extensive effort in one of North America's centers of Lepidopteran diversity, the San Pedro River riparian corridor in southeastern Arizona.

A resource-based model of edge effects

Edge effects can be caused by a variety of cascading ecological phenomena, from changes in microclimate to interactions with competitors or predators (see the mechanistic model presented in Ries et al. 2004). However, most of these factors integrate to cause predictable edge effects based on two main factors: (1) relative differences in habitat quality and (2) the distribution of key resources (Ries et al. 2004; Ries and Sisk 2004). By focusing on these two variables, we suggest that it is possible to predict how population density will change near edges for any species at any edge type. The model predicts that organisms should avoid edges adjoining non-habitat or lower quality habitats that offer only supplementary resources, they should show increased density near edges with higher quality habitat or habitat that contains complementary (different) resources, and they should show no response to edges adjoining similar quality habitat that offers only supplementary (similar) resources (Fig. 1). The more stark the contrast in habitat quality or resource division, the stronger the edge response should be (Ries and Sisk 2004). This model is a synthesis of ideas published in the edge literature; a detailed description of the underlying mechanistic framework is presented in Ries et al. (2004) and Ries and Sisk (2004). For this test of our model, information on habitat preferences and resource distribution (in this case, host and nectar plants) was used to generate predictions for 15 butterfly species at 12 different edge types within desert riparian habitats in southeastern Arizona. By applying this model to numerous butterfly species at multiple edge types, we created the

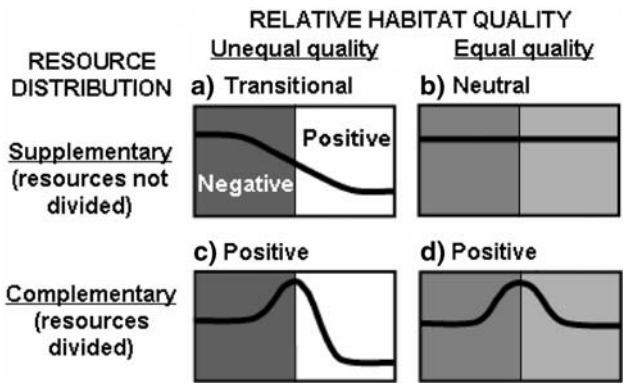

Fig. 1 Model predictions of edge responses are transitional (**a**), neutral (**b**) or positive (**c**, **d**) based on relative habitat quality and resource distribution. Lower habitat quality is indicated by a *white box*, while habitats of higher or equal quality are *shaded*. The same resources are either available in both habitats (supplementary), or different resources are divided between habitats (complementary). Adapted, with permission, from Ries and Sisk (2004)

opportunity not only to test the qualitative predictive power of the model (how often the edge responses predicted by the model are observed) but also to determine how strongly the two key model variables (habitat association and complementary resource distribution) correlate with the strength of observed edge responses.

Test system: butterflies in desert riparian habitat

Butterflies in desert riparian habitat present an ideal system for conducting an empirical test of the model. The structure of desert riparian habitat leads to a multitude of relatively abrupt and well-defined edges that vary from "classic" forest-grassland edges to more subtle edges, such as those between riparian grasslands and desert scrub. Butterflies are an excellent group for testing the general applicability of the model because much is known about their ecology, but they have received relatively little attention in the edge literature. For this study, we define edges as abrupt linear boundaries between two different habitat types, positive edge responses as increases in butterfly density near edges (relative to the interior of the habitat patch), and negative edge responses as decreases in butterfly density near edges.

This study took place along the Upper San Pedro River in southeastern Arizona, within the boundaries of the San Pedro Riparian National Conservation Area [SPRNCA, see Appendix 1a in Electronic Supplementary Material (ESM)], where grazing and agriculture have been excluded since 1987 (Kreuper et al. 2003). The Upper San Pedro River's riparian corridor exists as a two-tiered system with a primary floodplain and upland riparian zone surrounded by desert scrub (Appendix 1a in ESM). The primary floodplain is dominated by Fremont cottonwood (*Populus fremontii*) and Gooding's willow (*Salix goodingii*), which form a highly heterogeneous canopy structure with large openings throughout. The dominant woody vegetation in the upland riparian zone is mesquite (*Prosopis velutina*), although other shrubs are common. This zone also demonstrates a high degree of heterogeneity in canopy structure, ranging from open grasslands to dense riparian forests or "bosques". Intermediate between these two extremes are areas akin to open woodlands, where tall mesquite are abundant, yet sufficiently spaced to allow for the development of a thick herbaceous layer. To reduce the effects of internal heterogeneity, we classified the upland riparian zone into three habitat types: grassland (GRASS), mesquite-dominated forests (MES) and grassland-mesquite mixes (MIX). The surrounding desert scrub is characterized by widely-spaced, low shrubs with a rocky ground cover that typically supports only a sparse herbaceous layer. The juxtaposition of the cottonwood-dominated floodplain (CW), the three categories of upland riparian habitat (GRASS, MIX, and MES), and the surrounding desert scrub (DS) results in six combinations of adjacent habitat pairs of varying structural contrast (CW and GRASS, CW and MIX, CW and MES, GRASS and DS, MIX and DS, MES and DS). We considered edge responses separately on either side of the edges formed by these six habitat pairs, resulting in 12 edge types that were the focus of this study (Appendix 1b in ESM).

Material and methods

We established 17 study areas during a 3-year period (1999–2001) throughout the 70-km extent of the SPRNCA (Appendix 1a in ESM), with one additional site 50 km north of the boundary. Not all sites were sampled in all years due to the occurrence of wildfires. Most study areas were at least 1 km from the next closest area of the same edge type (Appendix 1a in ESM), although in one case, study areas were only 300 m apart (in 1 year only) and in two other cases, 500 m. For purposes of our analysis, each study area was considered to be one independent sample site within the boundaries of the SPRNCA. There were from two to six independent study areas established for each edge type in each year, with most edge types represented in four or five areas. Mesquite edge types were not surveyed in 2001.

Transects, placed perpendicular to the edge, consisted of contiguous 10 × 10-m plots that generally spanned both sides of the edge, extending up to 100 m into the interior of upland riparian habitat and 40–50 m into cottonwood and desert scrub habitat (Appendix 1b in ESM). There were one to three transects established for each edge type within each study area, with all transects for the same edge type located within 50–100 m of each other. Multiple transects for one edge type within a single area were not considered to be independent and were pooled for analysis. Each edge type in each year was represented by between three and 13 transects, with a mean of eight transects per edge type.

Butterfly surveys were conducted from mid-August through early October in 1999, 2000, and 2001. Three (in 2000, 2001) or four (in 1999) complete rounds of surveys were conducted during each year, with a survey round lasting 3–4 weeks. Surveys began at one end of the transect, with an observer surveying alternate plots to the end of the transect, then reversing direction and surveying the remaining plots on the way back. The starting point of each transect was alternated between rounds. Surveys were only begun when the sun was not obscured by clouds. Each 10 × 10-m plot was searched for 3 min, and all butterflies seen were identified and recorded. Nectaring and oviposition activities were recorded, including the plant species on which each activity occurred. At the end of each survey, the presence of each plant species that was a potential nectar

source was recorded. In order to identify the distribution of host plants, once each field season we conducted separate surveys on herbaceous plants. A 10 × 2-m area along the edge of each plot was searched to determine the presence or absence of ten herbaceous taxa identified as important local host plants, including *Aristolochia watsoni*, *Viguiera dentata*, *Helianthus annus*, *Matalea* sp., *Sarcostemma* sp., *Cassia leptocarpa*, *Cassia roemeriana*, *Lepidium thurberi*, *Sphaeralcae* sp., and *Sida* sp. Surveys of the woody host species *Atriplex* sp. and *Celtis* sp. were conducted once, in 2001.

Data analysis

Fifteen species were sufficiently abundant to permit detailed analysis. Data from survey rounds during peak flight periods, identified separately for each species, were pooled to arrive at a single density estimate for each plot in each year. Information on habitat preferences and resource distribution was used to generate predictions from our model (see Fig. 1). We used ANOVA to determine if there were significant differences in density for each butterfly species between each of the six pairs of adjacent habitat types. Edge plots were not used in this analysis in order to avoid confounding habitat preferences and edge responses. Where one habitat type supported equal or higher densities relative to the adjacent habitat type, it was necessary to determine whether host and nectar plant distributions were complementary or supplementary. We did this by calculating the relative probability of encountering nectar and host plants on the adjacent side of the edge. Given these parameters, a predicted edge response was generated for each species at each edge type. Empirical edge responses were determined to be positive, negative, or neutral based on finding a slope parameter significantly different from zero in a linear regression model. Because this study used plots within transects, which represent repeated measures along a non-independent sampling unit (Diggle et al. 1994), a mixed model was used with distance to edge as the fixed effect, study area as a random effect, and plots within transects specified as repeated measures (Littell et al. 1996). Examination of the residuals at varying distances indicated a decay in correlation strength as distance increased, so an autoregressive correlational structure was specified in the model (Diggle et al. 1994). The regressions were run with the number of transects in each area (one to three) used as a weighting factor.

For the subset of species/edge type combinations where we had sufficient data to make predictions, we compared those predictions to observed edge responses. For both generating and testing predictions, making a Type-II error (failing to detect an effect where one does in fact occur) has consequences as serious as a Type-I error. To try to balance these two types of errors, we judged an alpha level of 0.10 to be appropriate for capturing biologically relevant trends in habitat associations and edge responses. In addition, we considered results in the range of $0.10 < P < 0.30$ to be "indeterminate", and excluded them from further consideration because they provide little statistical basis for identifying or rejecting either habitat associations or edge responses. These cut-offs were used only to generate predictions and classify edge responses. The actual test of the predictive power of the model comes from comparing how often predictions match observations and from determining the strength of association between predictor variables and the observed edge responses. The P values resulting from these key tests can be considered individually to assess the strength of the support for the model. All analyses were done in SAS (v 8.2) or SAS-JMP (v 4.0.4) (SAS Institute, Cary, NC).

Model predictions

For this application of the general edge effects model, habitat preferences were assigned separately for each of the six habitat pairs based on a species having significantly higher densities in the interiors of one of the adjacent habitat types. While local densities can sometimes be a misleading indicator of local habitat quality (Van Horne 1983) due to factors such as source-sink dynamics, we use densities pooled across spatially replicated patches to broadly define general habitat associations (e.g., whether a species prefers MES over GRASS)—not to identify particular patches as being of particularly high or low quality. When there was a significant difference in butterfly densities in two adjacent habitat types, the habitat with the higher density was identified as "preferred", and the habitat with the lower density as "less-preferred". Habitat pairs were identified as being "equally preferred" when differences in density were not significant. For the determination of "equally preferred", we used a P value of 0.30 to minimize Type-II errors. However, when P values fell between 0.10 and 0.30, no predictions were generated because habitat preferences could not be clearly determined from our data. In order to generate predictions from our model in these cases, more field data on habitat preferences would be needed. The analyses used to assign habitat preferences are detailed in Appendix 2 (ESM).

Local nectar and host plants preferences (listed in Appendix 3 in ESM) were identified through a combination of efforts, including: (1) associations published in a local field guide (Bailowitz and Brock 1991); (2) conversations with James Brock, an area host plant expert; (3) our own nectaring and oviposition observations; (4) observations of eggs and caterpillars on candidate host plants made throughout our 3-year study. For each plot, the presence or

absence of each resource was recorded, and the overall proportion of plots containing each of the key resources was calculated for each habitat type within an area. We considered resource distribution to be complementary if either nectar or host plant resources were at least twice as likely to be encountered in the adjacent habitat. Otherwise, resources were listed as supplementary. This cut-off presented a reasonable break-point between cases where resources were similarly available on both sides and cases where resource distribution was starkly different (see Appendix 3 in ESM for details). For five species, we had only limited data on host plant distribution between some habitat pairs; in those cases, our determination of resource distribution was partially based on observations we made throughout the 3-year study. In these cases where data on resource use or distribution was limited, we identified confidence in our resource data as "low"; otherwise it was identified as "high". Confidence in resource distribution was subsequently examined to determine its influence on how well the model performed.

Qualitative comparison of predictions to observations

Edge response predictions were compared qualitatively to observations by building a 3×3 contingency table (Table 1) that tallied the number of times observations did or did not match predictions (e.g., how often did we see a positive edge response when one was predicted, etc.). When the predicted edge response was observed, the outcome was called "correct". Cases in which the model was incorrect were divided into two categories: "neutral" (a neutral result was observed where a positive or negative edge response had been predicted) or "wrong" (an unpredicted positive or negative edge response was observed) (Table 1). While both types of incorrect predictions indicate avenues for future model improvement, the approaches may be different for each. For example, some species are thought to be generally insensitive to edges (Wiens et al. 1985, Lidicker 1999) and identifying the prevalence of "neutral" responses may allow us to identify those species and the life history traits associated with edge insensitivity. In contrast, an unpredicted "wrong" response may be due to incomplete data on that species' resources relative to the focal edge type or to the presence of a dynamic not incorporated in the current model construction. By separating incorrect outcomes into these two categories, we can separately explore the implications of each.

To gauge overall model performance, we determined if the number of "correct" outcomes was more frequent than expected by chance. To do this, we performed two goodness-of-fit tests. The first compared the observed distribution of outcomes in the 3×3 table (Table 1) to an independent distribution among rows (predictions) and columns (observations). Residuals, adjusted to cell totals (as per Agresti 1996), were then examined to determine if there were more "correct" observations than would be expected by chance. We refer to this test as the "Residuals Test". We used Fisher's Exact Test to determine if those residuals were significantly different from zero. A second goodness-of-fit test examined the subset of cases where positive or negative edge responses were predicted to determine how often observed responses were in the predicted direction. We refer to this as the "Direction Test". We used a chi-square test to determine if observed responses were in the predicted direction more than 50% of the time (the proportion expected if results were randomly distributed). In addition, both the Residuals Test and the Direction Test were stratified by habitat type and species to allow an exploration of whether the model performed particularly well or poorly in particular habitats or for certain species.

Table 1 Evaluation of model performance

	Observation		
Prediction	–	0	+
–	Correct	Neutral	Wrong
0	Wrong	Correct	Wrong
+	Wrong	Neutral	Correct

A 3×3 contingency table illustrates cases where the model is correct (the predicted edge response was observed), wrong (an unpredicted positive or negative response was observed), or neutral (a neutral response was observed when a positive or negative response was predicted)

Quantitative comparison of predictions to observations

Although our model does not make specific quantitative predictions about the strength of edge responses (for example, predicting that densities will be twice as high at the edge vs. the interior), we specifically predict stronger edge responses when there are stronger differences in habitat associations and/or complementary resources in adjoining habitats (Ries and Sisk 2004). We therefore examined the strength of the relationship between the magnitude of the differences between habitat types for each of our two predictor variables (habitat association and resource distribution) and the slope of the measured edge responses. Differences in habitat association were calculated by subtracting, separately for each species at each edge type in each year, the density in the focal habitat from the density in the adjacent habitat. To be included in this analysis, differences in habitat associations within years need not have been statistically significant (however, the species must have shown a significantly different association between the two habitat types across years). Using this approach, we were able to look at the entire spectrum of

responses—from strongly negative, to weak or absent, to strongly positive. A mixed-model regression, with species as the random component, was performed.

To explore the impact of complementary resource distribution, we calculated the mean slope of all edge responses for species in the following three categories: (1) those with no habitat associations and where resources in the adjacent patch are only supplementary (so no edge response is predicted); (2) those with no habitat association, but for which a complementary resource was concentrated in the adjacent patch (so a positive edge response is predicted); (3) those with no habitat association and complementary resources were restricted to the adjacent patch (so a stronger positive edge response is predicted). We performed a mixed-model ANOVA with slope as the fixed variable and species as the random variable on the three groups (supplementary, complementary-concentrated, complementary-restricted).

Results

Empirical edge responses

All 15 species showed at least one edge response for at least one of the 12 edge types over the 3 years of study (results for each species at each edge type over all 3 years are given in Appendix 4 in ESM). However, there was substantial variation in responses, both across species and among edge types. Of the 15 species studied, 12 showed positive, neutral, and negative edge responses at one or more of the different edges. Most observed responses were neutral, with positive or negative responses observed 21% of the time (32% if statistically marginal cases are excluded). Where a species showed more than one significant edge response across years at the same edge type, edge responses were in the same direction 93% of the time (highlighted in Appendix 4 in ESM).

Model predictions

An example of how we used data to generate—and then test—predictions is illustrated for one species (*Phoebis sennae*) at the edge between CW and GRASS habitats (Fig. 2a–d). The first step in generating predictions was to consider habitat preference. *Phoebis sennae* prefers GRASS habitat (Fig. 2a). Similar comparisons were made for all 15 species at all six habitat pairings. A significant habitat preference was found in 53 cases ($P < 0.10$), no habitat preference was found in 44 cases ($P > 0.30$), and no predictions were possible in the 25 remaining cases, where P values fell between 0.10 and 0.30 (see Appendix 2 in ESM). When habitat was either equally or more preferred, information on resource distribution (complementary or supplementary) was necessary to make predictions. In the case of *P. sennae*, the host plant is confined to the CW habitat, while nectar sources are more equally distributed (Fig. 2b, c). This result means that their host plant represents a complementary resource when they are in a GRASS habitat, so we predict a positive edge response on both sides of the edge (Fig. 1). No information on resource distribution is necessary when habitat is less preferred (in those cases, edge responses are always predicted to be positive, see Fig. 1). Appendix 3 in ESM shows when resources were identified as complementary or supplementary, for cases where that information was necessary to make a prediction.

Comparing qualitative model predictions with field observations

We compared observed edge responses with model predictions for all cases where predictions were possible. As noted above, a positive edge response was predicted for *P. sennae* on both sides of the CW–GRASS habitat edge. Based on our data, we observed a positive response in the GRASS habitat (so a "correct" outcome), but a neutral response in the CW habitat (so a "neutral" outcome) (Fig. 2d). A tally of outcomes and the associated residuals are detailed in Table 2, both combined and stratified by habitat and species. For all habitats and species combined, the model was able to predict the observed edge response more often than expected by chance ($P = 0.01$), as indicated by the positive value for the adjusted residuals in the "correct" category for all habitat types combined (Fig. 3a). When the model was incorrect, it was 2.6-fold more likely that no response was observed when a positive or negative response was predicted, rather than observation of an unpredicted positive or negative ("wrong") response (Fig. 3a). For cases where a significant edge response was observed, the Direction Test showed the responses were in the predicted direction 70% of the time for all habitats combined ($P < 0.001$, Fig. 3b).

We also applied the Residuals and Direction Tests stratified by habitat. In these cases, sample sizes were too low to test for statistical significance, but the stratified comparisons indicated whether model performance was particularly good or poor in certain habitat types. Model performance was best in the upland riparian zone (GRASS, MIX, MES) and lowest in the CW and DS habitats (Fig. 3a). Model performance was also highest in the same habitats for the Direction Test (Fig. 3b) and again lowest for CW, with observed responses in the predicted direction only 17% of the time (Fig. 3b). We explore this result in greater detail below; however, in order to examine the relationship between the magnitude of habitat and resource differences, on one hand, and the magnitude of edge responses on the

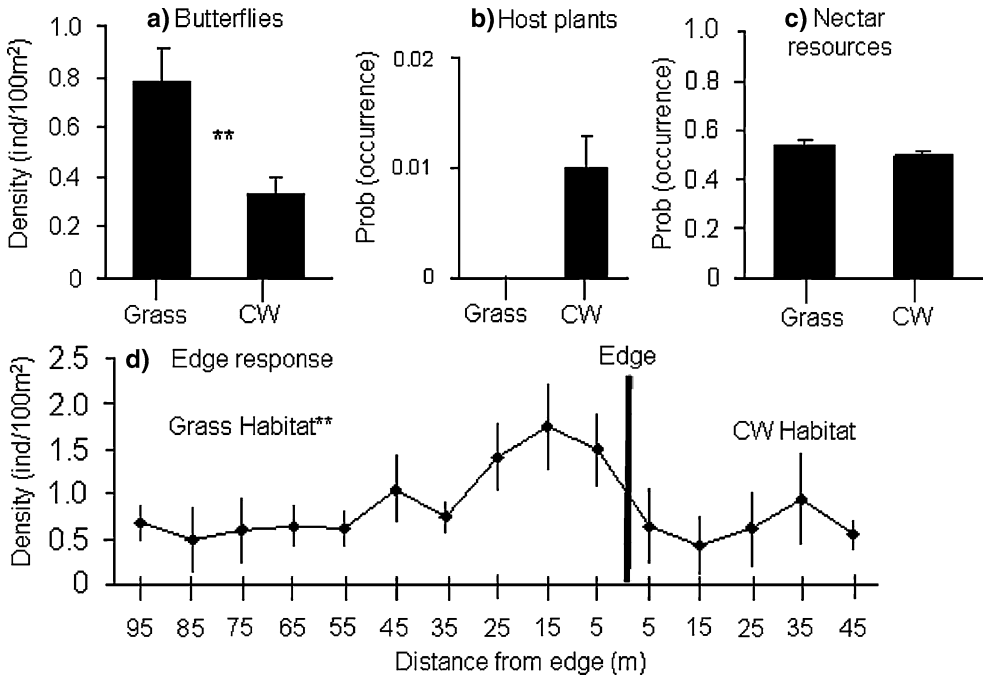

Fig. 2 An example of the evaluation of model performance for the edge responses of *Phoebis sennae* butterflies on either side of the Grasslands (*GRASS*)–Cottonwood (*CW*) habitat edge in Arizona, USA during 1999–2001. The observed distribution of butterflies (**a**), host plants (**b**), and nectar resources (**c**) suggest that *Phoebis sennae* prefers the GRASS habitat (**a**), but have complementary resources in the CW zone (**b**). The model therefore predicts a positive response at both edges (see Fig. 1c). The densities of *P. sennae* across the GRASS–CW edge (**d**) show that the model correctly predicted the positive edge response observed in GRASS habitat ($P < 0.05$), but not the neutral response in the CW habitat. Means and standard errors are shown with significant differences (**$P < 0.05$) indicated

other, further evaluations omit results from the CW habitat. Given this caveat, nine of the 14 species had more "correct" outcomes than expected by chance (Table 2). Inspection of the data revealed no influence of confidence of resource distribution ("low" or "high") on any outcomes (analysis not presented).

Comparing quantitative model predictions with field observations

There was a significant ($P < 0.0001$) positive relationship between the magnitude of the habitat preference and the measured slope in the edge model (Fig. 4). This result is consistent with the qualitative predictions of the model (that positive edge responses are expected in a less preferred habitat and negative edge responses are expected in a more preferred habitat—see Fig. 1). As the strength of habitat preferences increased, the magnitude of the slope of the edge responses also increased (Fig. 4). The results for complementary resource distribution were less clear. Only cases where complementary resources were entirely restricted to the adjacent habitat showed any trend towards positive edge responses ($P = 0.07$). In contrast, when complementary resources were available on both sides (although concentrated in the adjacent habitat), there was no trend towards positive responses at all ($P = 0.42$). Species showing no habitat preference and supplementary resources were predicted to have no edge response, and indeed the mean edge response slope for this group was also zero ($P = 0.31$).

Discussion

Edge responses for several butterfly species at a wide range of edge types were, when observed, largely predictable and consistent. This result strongly supports our general model of edge effects, the only currently available model that allows specific edge response predictions to be made. The use of this model helps make sense of much of the variability observed in systems with multiple species and multiple edge types. The model performed significantly better than expected by chance (Fig. 3a) and was able to predict the correct direction of edge responses about 70% of the time for this diverse assemblage of riparian butterflies (Fig. 3b). Earlier reviews (Ries and Sisk 2004; Ries et al. 2004) showed that the model was also successful for birds, plants and mammals, predicting the correct direction of observed edge responses 83, 91, and 83% of the time, respectively. These combined results suggest that many edge responses can be understood by considering habitat associations and resource distribution, rebutting previous conclusions that

Table 2 Comparison of model predictions to field observations. Evaluations of overall model performance are illustrated in Fig. 3

Prediction:	−			0			+			Residuals[c]		
Observation:[a]	−	0	+	−	0	+	−	0	+			
Model performance:[b]	C	N	W	W	C	W	W	N	C	C	N	W
All habitats	19	36	5	8	44	9	13	55	22	7.0	−1.5	−5.5
Cottonwood	0	2	0	6	15	2	5	14	1	−1.8	1.1	0.5
Grass	6	12	4	0	1	1	2	8	8	3.0	−0.0	−3.1
Mix	10	18	0	0	9	3	2	6	3	4.9	−0.9	−3.9
Mesquite	3	4	0	1	13	1	0	1	0	3.3	−1.1	−2.3
Desert scrub	0	0	1	1	6	2	4	26	10	−0.5	−1.1	1.5
Species summaries (cottonwood excluded)												
All species	19	34	5	2	29	7	8	41	21	8.6	−1.7	−6.9
Battus philenor	0	5	0	0	0	0	3	5	1	−0.7	0	0.7
Brephidium exilis	2	4	0	0	0	0	0	0	1	3.3	0	−3.3
Chlosyne lacinia	0	7	1	0	0	1	0	2	1	−1.4	1.0	0.4
Colias cesonia	1	2	0	1	6	0	0	1	0	1.2	−0.3	−0.9
Colias eurytheme	2	3	0	0	5	0	0	3	1	5.1	−1.4	−3.7
Danaus gilippus	1	4	0	0	1	0	0	3	0	1.3	−0.2	−1.1
Euptoieta claudia	4	0	0	1	2	0	0	0	0	3.9	−1.9	−1.9
Eurema nicippe	0	0	0	0	1	2	1	5	4	−1.3	0.5	0.8
Eurema proterpia	0	0	0	0	5	0	1	1	2	4.2	−2.4	−1.8
Libytheana carinenta	0	1	1	0	3	3	2	9	0	−4.3	0.9	3.4
Nathalis iole	0	0	2	0	5	0	0	1	0	1.5	−2.2	0.7
Pholisora catullus	0	0	0	0	0	1	1	2	2	−1.9	0.8	1.1
Phoebis sennae	1	2	0	0	1	0	0	3	9	6.1	−0.6	−5.4
Pontia protodice[d]	1	0	0	0	0	0	0	0	0			
Pyrgus albescens	7	6	1	0	0	0	0	6	0	1.5	0	−1.5

[a] A tally of observed edge responses separated by habitat type and species where negative (−), neutral (0), and positive (+) edge response predictions were made

[b] Model performance is separated into cases where a prediction was correct (C), an unpredicted neutral response was observed (N), and cases where an unpredicted "wrong" positive or negative response was observed (W)

[c] Adjusted residuals showing the relative occurrence of each outcome are also shown (positive residuals indicate an outcome happened more frequently than expected by chance and vice-versa)

[d] Residuals could not be calculated due to a lack of data

edge effects are idiosyncratic and difficult to understand or predict. In these studies, the majority of negative edge responses can be attributed to species avoiding edges with less-preferred habitat. Positive edge responses can be largely explained by increased densities near a preferred, adjacent habitat, or by proximity to resources restricted to adjacent patches.

We found a significant relationship between the strength of the habitat association and the strength of the edge response. Our model predicts that species should decrease in abundance as they approach edges with less preferred habitat, but may "spill over" into the adjacent habitat, causing a positive edge response (Fig. 1a). In such cases, the magnitude of the difference in habitat preference should be reflected in the strength of the edge response (Sisk and Ries 2004), and indeed this was true for butterflies in this study (Fig. 4). These results support the use of habitat associations as a predictor in the model and suggest that the strength of habitat preferences could be used to infer the magnitude of edge responses.

The relationship between complementary resource distribution and the strength of the edge response was not so clear. In fact, complementary resource distribution was not a useful predictor except in situations where the complementary resources were entirely restricted to the adjacent habitat. Although complementary resource distributions (also known as cross-boundary subsidies) have been suggested as mechanisms underlying edge responses (Fagan et al. 1999), no empirical work has attempted to quantify how divided the resources must be to have an impact on edge responses. This study suggests that, at least for butterflies, the separation of resources must be very stark in order to trigger positive edge responses. When conducting future tests of the model, researchers should consider being more conservative than we were in defining what constitutes a complementary resource.

In cases where model predictions were incorrect, it was more than twice as likely that no response was observed where a positive or negative response had been predicted, as opposed to cases where unpredicted positive or negative edge responses were observed. This general trend was observed in past tests of the model for bird, mammal, and plant taxa (Ries et al. 2004), suggesting that the model is prone to over-predicting directional edge responses but that it is quite successful in predicting the nature of directional responses (positive or negative) when they occur. This

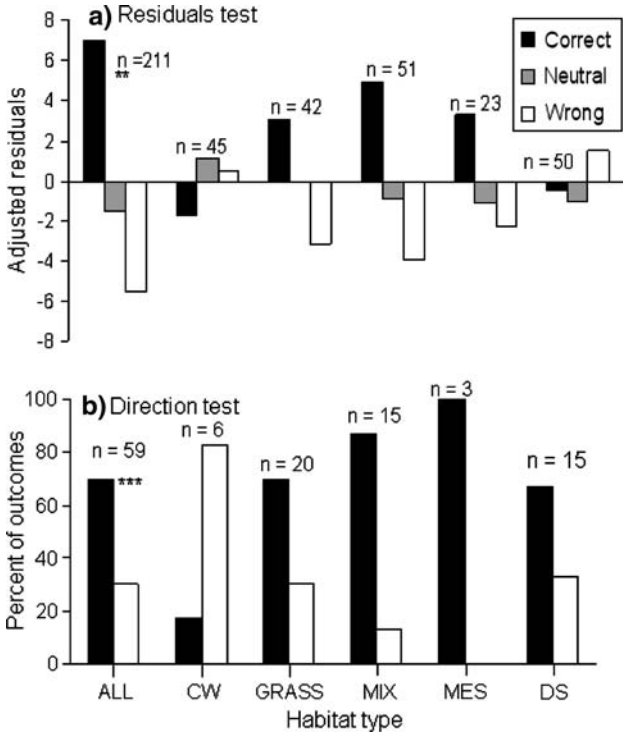

Fig. 3 Evaluation of model performance using the Residuals Test (**a**) and Direction Test (**b**) for 15 butterfly species at 12 edge types within five different habitats. Responses are pooled for all species among habitats (*ALL*) and stratified by habitat type [*CW*, *GRASS*, mesquite-dominated forests (*MES*), grassland-mesquite mixes (*MIX*), surrounding desert shrub (*DS*)]. The residual test (**a**) indicates whether the correct, neutral, or wrong responses (see Table 1) were observed more (positive values) or less (negative values) often than expected by chance. The *P* value is based on Fisher's Exact Test. The Direction Test (**b**) indicates the percentage of times the direction of observed edge responses was correctly or wrongly predicted. The *P* value is based on a χ^2 test that compares observed percentages to an expected value for random response (50%). $^{**}P < 0.05$, $^{***}P < 0.01$. Statistical tests were only carried out for the ALL category due to low sample sizes when stratified by habitat type

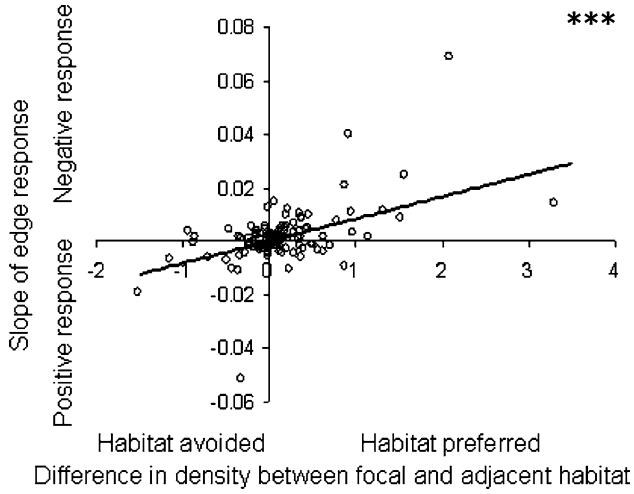

Fig. 4 The relationship between differences in individual density from focal to adjacent habitats (from strongly preferred to strongly avoided), and the slope of the edge response for species with supplementary distribution. All responses were included, regardless of whether the habitat associations for that year where significant or not, so that a full spectrum could be observed. Note that a positive slope for an edge response indicates a negative edge response, and vice-versa. $^{***}P < 0.0001$, value based on a mixed-model regression

result suggests that model improvement may hinge on an improved understanding of the ecological factors that lead to edge insensitivity.

Insensitivity to edges could be caused by physical factors, such as edge orientation and edge contrast (Ries et al. 2004), or species-specific factors, such as body size or mobility (Wiens et al. 1985). Despite the popularity of classifying certain species as edge sensitive or insensitive, it is currently impossible to say which species are truly insensitive to the presence of habitat edges (Ries et al. 2004). Only species that consistently fail to show edge responses where they are predicted to occur should be considered edge-insensitive. Using our model, these outcomes are represented by the two "neutral" cells in Table 1, in contrast to the center cell, where a neutral result is both predicted and observed. However, any model that uses a biological basis to predict when edge responses should occur could be used as a framework for identifying edge-insensitive species. Despite the current difficulty in classifying species as edge sensitive or insensitive, to do so would represent a significant advance in the study of edge effects. If common traits underlying edge insensitivity could be found, then model predictions could be significantly enhanced. For instance, Brand (2004) found that the likelihood of birds exhibiting edge responses was associated with body size, incubation period, and nest location and type.

Although observed edge responses were rarely in the opposite direction of those predicted (i.e., there were few "wrong" predictions), it is important to examine these results and determine their potential causes. The model did not do equally well in all habitats (Fig. 3a) or for all species (Table 2). As noted above, the model performed poorly in the CW habitat, with observed responses in the predicted direction only 17% of the time (Fig. 3b). One factor that clearly distinguished the CW from the upland habitat was its internal heterogeneity, which has been suggested as a factor influencing edge responses in birds (Noss 1991). Heterogeneity was addressed in the upland riparian habitat by separating it into three classes, based on canopy structure. However, we elected to consider the CW zone as a single habitat type despite its highly heterogeneous nature. In retrospect, it may have been more appropriate to separate the CW habitat into several classes based on canopy cover, similar to what was done in the upland area. This finding suggests that the initial way that habitat patches are defined within a landscape can influence the definition of edges and our ability to predict effects. Indeed, model performance is

profoundly influenced by a researcher's ability to define landscape elements in a way that is meaningful for the focal species. Model performance was also weak in the DS habitat (Fig. 3a) although observed edge responses were generally in the predicted direction (Fig. 3b). Unlike the CW habitat, the DS habitat has a simple structure of widely dispersed low shrubs, so internal heterogeneity is not a likely explanation. One possible factor is the low overall density of butterflies in this habitat type, which may make gradients more difficult to detect.

Model performance differed among species, with the model performing well (based on observing more "correct" responses than expected by chance) for nine of the 14 species (Table 2). For the remaining five species it is possible there was a gap in our knowledge about the primary local host or nectar plants. Alternatively, there may have been other resources that were driving those species' distribution patterns that were not considered here, such as the availability of roosting sites, minerals, or water (Dennis 2003). More detailed ecological studies of those species' critical resources and their distribution may help resolve why model performance was poor for these species. Using this modeling framework offers an opportunity to focus future studies on species whose edge responses are not easily explained and where more complex ecological interactions may be occurring (see Ries et al. 2004 for a discussion of future research directions).

A knowledge of local resources is particularly crucial for identifying complementary resource distribution. Our results suggest that identifying complementary resources only improved model predictions when resources were entirely restricted to the adjacent habitat, and even in those cases there was substantial variation in results. Although this mechanism is well supported in the edge literature (Fagan et al. 1999; Ries et al. 2004), the best studied examples involve cases where resources are almost completely partitioned between adjacent habitats (for example, brown-headed cowbirds are well-known edge exploiters who parasitize the nests of forest birds but forage in adjacent livestock pastures). Further research is needed to determine how the degree of segregation of complementary resources influences edge responses. This research will affect how conservative one should be when defining a resource as complementary.

Despite the difficulty we had effectively using complementary resource distribution to predict positive edge responses, it is worth noting that the species which we identified as having no difference in habitat preference between adjacent habitat pairs showed only significant positive edge responses or no edge response, never a negative edge response. Under these circumstances, the model only predicts positive or neutral edge responses with the critical difference in the prediction being due to whether complementary resources are present or not (Fig. 1c, d). The model never predicts a negative response under any circumstances, and indeed we never observed negative responses in the field. The congruence between model and empirical results suggests that the biological basis of the model construction is valid, while the variability in results suggests that we did not always do a good job of identifying complementary resources in this study system. The unpredicted positive responses seen at edges between habitats where species showed that no clear preference could have been due to the presence of unidentified complementary resources. Conversely, the many neutral edge responses we observed in cases where we predicted positive responses may indicate that the complementary resources we identified were actually supplementary or unimportant. Clearly, the correct identification of resources and determinations about their spatial distribution represent a challenging component of the model. While habitat associations are often known and generally consistent among regions, local resource use—for butterflies and other animal taxa—can vary and may require a more detailed knowledge of the biology of focal species.

Conclusions

Our study suggests that edge responses are more predictable and consistent than is commonly believed. At first glance, the 267 edge responses we report in Appendix 4 (in ESM) for 15 butterfly species at 12 edge types over 3 years may seem like an intractable list of conflicting results that are not readily interpretable; however, when viewed within the conceptual framework of our predictive edge effects model, many of the results make ecological sense. Negative edge responses can be largely attributed to the avoidance of a non-preferred habitat, while positive responses are due to increased access to resources near the edge of a preferred habitat or to particular complementary resources that are confined to the adjacent patch. Although we detected many more neutral edge results than predicted, when multiple edge responses were observed for the same species at the same edge type, they were remarkably consistent. Our results highlight the need for a better understanding of neutral edge responses, and they suggest future avenues of research that could identify factors, including landscape variables and species-level traits, that may underlie edge insensitivity. Our modeling framework makes it tractable to explore factors, both extrinsic and intrinsic to the study species, which are associated with the likelihood of observing a predicted edge response, allowing a more focused exploration of mechanisms driving edge dynamics.

Our model tests revealed that habitat associations, the most widely available type of ecological information, are

consistent and effective predictors of edge responses. These tests also indicated that complementary resource distribution is an important factor influencing response, but that obtaining this information may be more challenging than expected and that resource separation may have to be quite stark before its influence on butterfly distributions is detectable. Although the application of our model to riparian butterflies involved consideration of host and nectar plant resources, the model could be applied to a wide variety of situations where habitat associations and general resource distributions are known. Previous tests of the model based on literature reviews showed that it was successful in predicting responses for birds (Ries and Sisk 2004), mammals, and plants (Ries et al. 2004), suggesting that this model has general applicability. Despite decades of study and hundreds of published reports, a coherent, general framework for understanding edge responses has remained elusive because most studies were largely descriptive, with no underlying conceptual model to put variable observations into a theoretical context (Murcia 1995; Cadenasso et al. 2003; Ries et al. 2004; Ries and Sisk 2004; Ewers and Didham 2005). This study represents an important step forward in placing edge responses into a predictive framework, and develops a blueprint for future studies by suggesting which factors should be taken into account when examining variation in edge responses.

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ECOLOGICAL RESPONSES TO HABITAT EDGES: Mechanisms, Models, and Variability Explained

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Key Words ecological boundary, ecotone, edge effect, effective area model, core area model, habitat fragmentation

■ **Abstract** Edge effects have been studied for decades because they are a key component to understanding how landscape structure influences habitat quality. However, making sense of the diverse patterns and extensive variability reported in the literature has been difficult because there has been no unifying conceptual framework to guide research. In this review, we identify four fundamental mechanisms that cause edge responses: ecological flows, access to spatially separated resources, resource mapping, and species interactions. We present a conceptual framework that identifies the pathways through which these four mechanisms can influence distributions, ultimately leading to new ecological communities near habitat edges. Next, we examine a predictive model of edge responses and show how it can explain much of the variation reported in the literature. Using this model, we show that, when observed, edge responses are largely predictable and consistent. When edge responses are variable for the same species at the same edge type, observed responses are rarely in opposite directions. We then show how remaining variability may be understood within our conceptual frameworks. Finally, we suggest that, despite all the research in this area, the development of tools to extrapolate edge responses to landscapes has been slow, restricting our ability to use this information for conservation and management.

INTRODUCTION

The edges between habitat patches are often ecologically distinct from patch interiors, and understanding how ecological patterns change near edges is key to understanding landscape-level dynamics such as the impacts of fragmentation. Landscapes are often viewed as patches of habitat and nonhabitat (Figure 1*a*), and

thus "edge effects" have often been conceptualized as an ecological change that is due to moving away from the "core" area of a patch and not directly linked to landscape context. In fact, landscapes exist as mosaics of several different patch types (Figure 1*b*), so understanding the ecology of habitat edges requires understanding the complex influences that each different adjacent patch has on a focal patch. As patches become smaller and more irregularly shaped, they become increasingly dominated by edge habitat. Therefore, understanding the ecology of habitat edges is critical both for landscape ecology and for large-scale conservation and management decisions.

Because of their importance and ubiquity, habitat edges are one of the most extensively researched areas in ecology. Most edge studies measure ecological patterns, such as changes in abundance or fitness with respect to the edge. However, the literature covers a wide range of topics, including the factors that maintain or change the position of edges in a landscape (e.g., Arris & Eagleson 1989, Bowman & Fensham 1991, Allen & Breshears 1998, Callaghan et al. 2002, Klasner & Fagre 2002); the identification and measurement of edges within remotely sensed data (e.g., Fortin 1994, Choesin & Boerner 2002, Fagan et al. 2003); the impact of edges on migration through their role in mediating dispersal (e.g., Stamps et al. 1987, Haddad 1999, Ries & Debinski 2001, Schultz & Crone 2001, Schtickzelle & Baguette 2003); and the evolutionary impacts of edges on populations, including speciation (e.g., Smith et al. 1997, Schilthuizen 2000) and the maintenance of hybrid zones (Young 1996). For this review, we focus on ecological responses, particularly species abundance patterns, to the presence of habitat edges. Our goal is to understand the mechanisms that underlie those responses and to place the research into a conceptual framework that helps explain reported patterns and variability. Further, we explore how these patterns may help us understand large-scale dynamics.

Edges are generally defined as boundaries between distinct patch types, so the identification of edges depends on how patches are defined within a landscape. Patch definition can occur at a variety of scales, from patches of different species of plants within a meadow to major biomes within continents (Cadenasso et al. 2003). To limit our scope, we focus on patches of different vegetation or land-use classes (i.e., forests, meadows, scrub, agriculture, urban areas, etc.) within terrestrial landscapes. We refer to any variable that increases near edges as having a positive edge response, a variable that exhibits no pattern as having a neutral response, and a variable that decreases near edges as having a negative edge response (see Figure 2).

The earliest reference to edge-related ecology is attributed to Clements (1907), who introduced the term "ecotone." The influence of these "zones of transition" on wildlife has been noted for decades, with Leopold (1933) using the term "edge effect" to describe the increase in game species in patchy landscapes. Other early accounts of increased diversity near edges (Lay 1938, Johnston 1947) added to the general conception that edges were good for wildlife, and their creation was often recommended in management (Harris 1988, Yahner 1988). The view of edges as

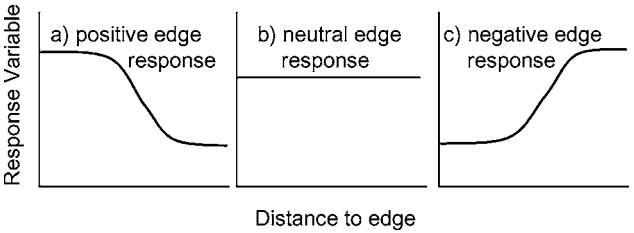

Figure 2 Three classes of ecological edge responses with respect to distance from the closest habitat edge. Responses are generally categorized as (*a*) positive edge responses, where the variable of interest increases near the edge; (*b*) neutral responses, where there is no pattern with respect to the edge; and (*c*) negative responses, where the variable decreases near the edge.

largely beneficial began to change by the late 1970s with the discovery that some birds were experiencing higher rates of nest predation and parasitism near forest edges (Gates & Gysel 1978, Chasko & Gates 1982). This pattern, coupled with increased bird numbers near edges, led many to view forest edges as "ecological traps" (Gates & Gysel 1978) and to suggest that this phenomenon may contribute to the decline of songbirds (Brittingham & Temple 1983, Wilcove 1985). In addition, edges became associated with decreased quality for habitat specialists (Mills 1995, Burke & Nol 1998) and the invasion of exotic species into habitat reserves (Morgan 1998, Honnay et al. 2002). These issues helped form the modern perception of edges, especially anthropogenic edges, as undesirable landscape features (Harris 1988, Saunders et al. 1991).

The past two decades have seen a flood of edge research on a wide range of organisms (Table 1) at an increasingly diverse number of edge types. In addition, a growing focus on mechanisms that underlie edge effects (Murcia 1995, McCollin 1998, Fagan et al. 1999, Cadenasso et al. 2003) has led to many empirical investigations of these mechanisms (e.g., Kingston & Morris 2000, Fletcher & Koford 2003, Kristan et al. 2003). However, highly variable response patterns (Murcia 1995, Villard 1998, Sisk & Battin 2002) create the impression that edges are associated with idiosyncratic responses to disparate ecological phenomena (Ehrlich 1997). Yet much of the difficulty in grappling with the edge literature stems from the lack of a framework for understanding the patterns reported (Murcia 1995, Cadenasso et al. 2003) or comparing responses at the different edges present in a landscape (Ries & Sisk 2004). Determining how edge response patterns manifest at broader scales is also difficult, limiting most studies' utility for management and conservation (Sisk & Haddad 2002, Sisk et al. 2002, Battin & Sisk 2003). To clarify these issues, we present four major sections for this review:

1. A mechanistic model of edge responses. We synthesize ideas from the literature into a conceptual model of the fundamental mechanisms underlying

TABLE 1 A summary from a subset of studies measuring responses at forest edges showing the number of times positive, negative, neutral, or mixed results were observed[a]

Taxon	Number of studies[b]	Response variable	Pos	Neg	Neutral	Mixed[c]
Birds	10	Richness/diversity	2	0	3	5
	32	Abundance by species[d]	86	49	344	28
Plants	13	Richness/diversity	7	1	2	3
	16	Abundance by species[d]	85	30	167	9
Mammals	1	Richness/diversity	0	1	0	0
	20	Abundance by species[d]	12	6	25	9
Invertebrates	8	Richness/diversity	1	0	4	3
	10	Abundance by species[d]	6	7	70	11
Herps	1	Richness/diversity	0	1	0	0
	5	Abundance by species[d]	0	6	13	2
Abiotic	20	Several[e]	22	8	21	18

[a]Only studies that measured responses within forest edges adjacent to open habitat and met certain design criteria (see text) were included. See Appendix 1a for specific studies used.

[b]Only studies that met certain design criteria were included, see text for details.

[c]Studies reported more than one response (e.g., positive and neutral) for the same response variable when analyses were stratified by some factor.

[d]Summed tallies of all species reported in each study.

[e]For example, temperature, light levels, humidity, wind, soil properties, etc.

edge response patterns and describe the empirical evidence supporting each component of that model.

2. A predictive model of edge responses. We review a model that predicts how abundances change near edges and assess the ability of that model to account for variability described within the literature.
3. Interactions affecting edge responses. We review studies that identify ecological factors that interact with edge responses and determine how that variability can be understood within the framework of the above models.
4. Extrapolating edge responses to larger scales. We explore our ability to use edge response patterns to understand the distribution of organisms in heterogeneous landscapes.

To determine the strength of evidence for suggested patterns and mechanisms, we reviewed over 900 empirical papers on terrestrial edge responses located through database searches and from citations within papers. From those papers, we selected a subset for review on the basis of the following criteria: (*a*) distance to edge was an explanatory variable for analysis, (*b*) there was a minimum of three sampling replicates, (*c*) basic habitat descriptions were given for both sides of the edge, and (*d*) the adjacent patches among replicate study sites were similar in

structure (i.e., all forest or all open). We imposed these criteria to ensure that studies were both comparable and relatively rigorous. Because studies on avian nest success have been thoroughly reviewed (see Paton 1994, Hartley & Hunter 1998, Lahti 2001, Chalfoun et al. 2002b), we did not include those empirical papers but instead present a synthesis of those reviews. These criteria resulted in 263 core papers used for our review of the empirical literature.

A MECHANISTIC MODEL OF EDGE RESPONSES

A Conceptual Framework

Researchers have invoked a broad range of mechanisms to explain changes in organism abundance near edges (Wiens et al. 1985, McCollin 1998, Fagan et al. 1999, Lidicker 1999, Cadenasso et al. 2003), yet a comprehensive framework has remained elusive (Murcia 1995, Ries & Sisk 2004). Here, we present a unified model of the mechanisms underlying edge effects on the abundance of organisms. From our review of the literature, we identified four fundamental mechanisms that change organismal abundance patterns across habitat edges: (*a*) ecological flows, (*b*) access to spatially separated resources, (*c*) resource mapping, and (*d*) species interactions. Ecological flows involve the movement of material, organisms, or energy between patches (Wiens et al. 1985, Cadenasso et al. 2003). Access to spatially separated resources may be enhanced near edges for organisms whose required resources are found in multiple habitat types (Leopold 1933, Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). These first two mechanisms, flows and access, fundamentally alter habitat quality of edges relative to patch interiors. Habitat edges have maximum exposure to flows from adjacent patches and are the ideal location to gain access to spatially separated resources.

The final two mechanisms, resource mapping and species interactions, represent general ecological dynamics that, although not restricted to edges, are important components in an overall framework of how edges influence distributions. Resource mapping occurs when an organism's distribution reflects that of its resources. Species interactions describe any interspecific relationship that influences one or both species. In some cases (e.g., predator-prey interactions), an interaction constitutes resource use from one organism's point of view, causing overlap between the categories of resource mapping and species interactions. To avoid confusion, we define predator dynamics as species interactions from the perspective of the prey but resource mapping from that of the predator. Mutualisms and competition are considered under the category of species interactions. Although these four mechanisms capture most dynamics that influence edge responses, there may be some taxon-specific factors that do not fit easily into this, or any, general framework. For instance, the geometry of packing bird territories into patches may cause decreases in bird abundances near edges (passive displacement) that are not based on any change in habitat quality (King et al. 1997, Ortega & Capen 1999, Fletcher & Koford 2003).

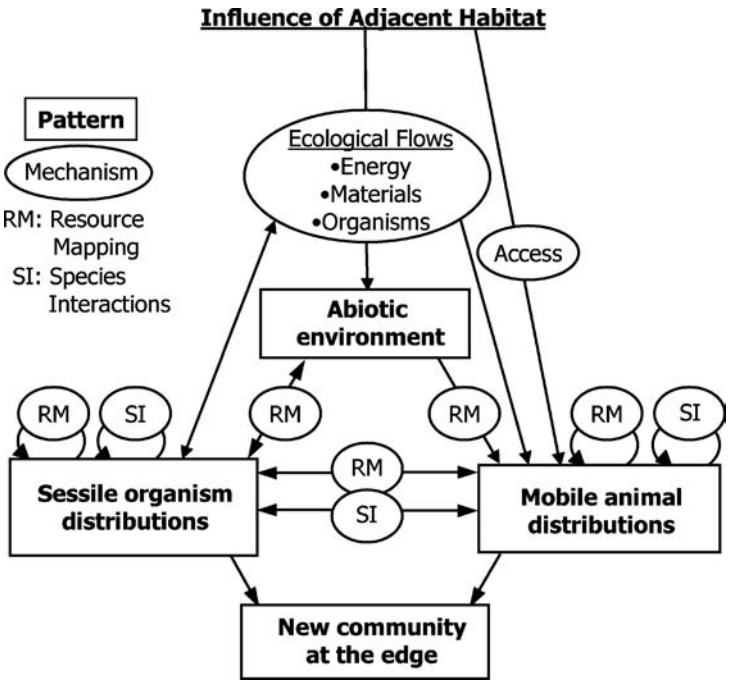

Figure 3 A mechanistic model describing the different pathways by which the distributions of organisms and, ultimately, community structure are altered near habitat edges. Patterns in the abiotic environment, mobile and sessile organism distributions, and community structure (*boxes*) are influenced by four fundamental mechanisms (*ovals*). Ecological flows of energy, material, and organisms across the edge influence the abiotic environment as well as organismal distributions. Mobile organisms whose resources are spatially separated can gain better access by being near edges. Organisms map onto changes in the distribution of their resources. Changes in species' distributions near edges can lead to novel species interactions that can further influence abundance and distributions. All these changes in species distribution lead to altered community structure near edges.

Figure 3 illustrates how these four mechanisms influence patterns in organismal distributions near habitat edges. We separate organisms into mobile and sessile groups because different pathways occur for each (specified below). Ecological flows influence mobile and sessile organisms directly by providing a source of materials and immigrants across edges. Indirect influences can also occur via organisms mapping onto changes in the abiotic environment near edges. However, only sessile organisms can feed back and directly influence ecological flows and the abiotic environment (note double-sided arrows in Figure 3 for those pathways). This feedback can occur either through changes in edge architecture that influence the permeability of the edge (Didham & Lawton 1999, Cadenasso et al. 2003)

or by creating a gradient that affects the abiotic environment. Another factor that differentiates mobile from sessile organisms is that only mobile organisms are known to actively gain access to spatially separated resources in adjacent patches. Some sessile organisms may also demonstrate such responses if advantages at the edge can be realized via, for example, root or branch growth, but we are not aware of any examples demonstrating this effect. Instead, sessile organisms can gain access to resources associated with adjacent patches by being located near edges that receive flows from neighboring patches. Within the current edge literature, the categories of mobile and sessile organisms separate animals from plants and lichens, but that need not always be the case (for instance, many sessile aquatic organisms are animals). However, owing to this current dichotomy in the terrestrial literature, we formulate the bulk of our remaining discussion with respect to research on animals (mobile organisms) and plants or lichens (sessile organisms).

Finally, any change in a species' distribution may have cascading effects throughout the community (Figure 3). For example, changes in abiotic conditions near a habitat edge may lead to the establishment of new plant species, and previously absent animals may map onto these new resources, leading to novel interactions affecting multiple taxa and, ultimately, changing overall community structure (Figure 3). Below we review the evidence for each of the four mechanisms and, where possible, show how effects cascade throughout the community.

Empirical Evidence for Underlying Mechanisms

ECOLOGICAL FLOWS Ecological flows from adjacent habitat patches are a key mechanism underlying the distinction between edge and interior zones. The rate of ecological flows between patches is a function of edge permeability, the degree to which a given flow can penetrate the boundary between two patches. Edges can amplify, attenuate, or reflect ecological flows (Strayer et al. 2003). Edge permeability is strongly influenced by the architecture of the edge, largely on the basis of plant structure (Cadenasso et al. 2003). Changes in overstory cover can affect vertical penetration of light into a patch (Turton & Sexton 1996, Didham & Lawton 1999, Dignan & Bren 2003a), which may, in turn, affect temperature and humidity levels near the edge. The relative concentrations of energy, materials, and organisms on either side of the edge also affect flow rates. Materials that move passively may naturally diffuse to areas of lower concentration, but mobile organisms can move against natural gradients, making net flows more difficult to predict.

A number of studies have documented ecological flows from one patch into another. Microclimatic changes have been widely documented (e.g., Matlack 1993, Cadenasso et al. 1997, Burke & Nol 1998, Meyer et al. 2001) and are influenced by differential movement of light, heat, moisture, and wind from one patch to another (Weathers et al. 2001). The result of these differential flows is that environmental conditions near edges are often intermediate between conditions in both adjacent patch interiors. For instance, forest edges near open habitat are hotter, drier, and lighter than the forest interior (Chen et al. 1999). Conversely, open habitat near

forest edges experiences increased shading, leading to lower temperatures and higher humidity (Cadenasso et al. 1997). Materials can be moved into adjacent habitat through diffusion, deposition, or the flow of animals (Cadenasso et al. 2003). Movement of animals across edges is widely documented in studies that quantify how edges mediate dispersal or influence movement direction (Sakai & Noon 1997, Haddad 1999, Ries & Debinski 2001, Schultz & Crone 2001, Matthysen 2002, Schtickzelle & Baguette 2003). The flow of plant propagules (seeds and pollen) across habitat edges has been demonstrated, but has received less study (Cadenasso & Pickett 2001, Cubiña & Aide 2001). In some cases, edges can act as relatively impermeable barriers that cause the accumulation of organisms or materials at the edge (e.g., Desrochers & Fortin 2000).

ACCESS Access is the other key mechanism that separates the quality of edge habitat from interior zones. When resources are spatially separated between two adjacent patches, edges provide maximum access to both resources (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). In his explanation of why edges should harbor higher densities of animals, Leopold (1933) used the example of bobwhite quail (*Colinus virginianus*), which use four different habitat types: forest, brushland, grassland, and agricultural fields. He suggested that quail should occur at higher densities in landscapes in which these four habitats are highly interspersed. In another early example, aspen experienced the heaviest outbreaks of a leaf-mining insect (*Lithocolletis salicifoliella*) near stands of coniferous trees, which are used as the insects' overwintering sites (Martin 1956). In perhaps the best-known example, brown-headed cowbirds (*Molothrus ater*), which parasitize the nests of forest-dwelling songbirds but forage in open pastures, often increase in abundance near forest edges (Lowther 1993). Access to different habitat types may be especially important to animals whose juvenile and adult forms have different habitat requirements (Martin 1956, Ponsero & Joly 1998). However, one must distinguish between cases in which resources in adjacent patches are different (complementary) from cases in which adjacent patches contain the same (supplementary) resources (Dunning et al. 1992), because in the latter case no edge response is expected.

RESOURCE MAPPING Resource mapping influences species distributions through more pathways than any other mechanism in our model (Figure 3). Any edge-related change in the distribution of an organism's resources may result in a concordant change in that organism's distribution. Although resource mapping is the most frequently studied mechanism, most studies are correlational and fail to establish that the variables being measured influence the abundance and distribution of the focal organism.

Both plants and animals map onto abiotic gradients, with microclimate (e.g., solar radiation, temperature, humidity, soil moisture) the most extensively documented. Several studies suggest that increased light levels near the forest edge cause changes in the plant community (Wales 1972, Honnay et al. 2002,

Watkins et al. 2003), whereas studies on plant responses to nutrient gradients are rarer. Researchers have documented relationships between animal distributions and microclimate gradients (Burke & Nol 1998, Haskell 2000, Brotons et al. 2001, Fernandez-Juricic 2001, Schlaepfer & Gavin 2001). Lichens mapping onto tree distributions and liverworts mapping onto downed log distributions (Moen & Jonsson 2003) provide rare examples of sessile organisms mapping onto the distribution of other sessile organisms.

The most frequently studied mechanism for edge effects is resource mapping by animals onto plants, most commonly the relationship between bird distributions and vegetation structure, although most studies have not found evidence to support this mechanism (e.g., Ortega & Capen 1999, Fernandez-Juricic 2001, Beier et al. 2002, Fletcher & Koford 2003). Most of these studies, however, do not independently establish which vegetation characteristics are most directly related to bird distributions before they test for a correlation with distance to the edge. This approach limits the usefulness of these studies because animals are not expected to map onto gradients that do not influence the quality of their habitat. Kristan et al. (2003) provide a rare example of a study that independently tested the importance of different vegetation characteristics on bird and mammal distributions. They examined whether changes in those vegetation features near habitat edges could account for observed edge effects. They found that the abundance of two bird species and one mammal tracked changes in vegetation with respect to the edge, while another three species showed edge responses that were not related to vegetation (Kristan et al. 2003).

Animals mapping onto the distributions of other animals is also well studied. Spotted owls (*Strix occidentalis*) illustrate a clear example of a species whose edge response patterns are directly related to those of their prey. Spotted owls show increased abundances near edges when wood rats (*Neotoma* sp.) serve as their main prey (Zabel et al. 1995, Ward et al. 1998). Wood rats are more abundant at edges because they flow into forests from neighboring clearcuts, their primary habitat (Sakai & Noon 1997). In contrast, owls show no edge effect when their main prey base is flying squirrels (*Glaucomys sabrinus*), a species that shows no edge effect (Zabel et al. 1995). These and other examples demonstrate that organisms map onto gradients in their resources, but that researchers must identify the variables that most influence habitat quality before attempting to relate those variables to edge effects.

SPECIES INTERACTIONS Interactions in which one organism benefits at the expense of another (predation, parasitism, herbivory) are the most extensively studied class of species interactions within the edge literature, with the greatest attention paid to predation on bird nests. Edges are associated with increased nest predation and parasitism rates for birds, although most studies have found no edge effect on nest success, and a few have even found a decrease (see Paton 1994, Lahti 2001, Chalfoun et al. 2002b for reviews). These patterns may be influenced by the fact that most studies were conducted in only a few biogeographic regions (Tewksbury

et al. 1998, Sisk & Battin 2002). Parasitism is also higher at edges for some amphibians (Schlaepfer & Gavin 2001) and mammals (Wolf & Batzli 2001). There is less evidence for consistent effects of predation and parasitism on invertebrates. Bird predation rates on the mantid species *Stagmomantis limbata* increased near edges, whereas parasitism rates were unaffected (Ries & Fagan 2003). Conversely, viral infections decreased near edges for the tent caterpillar *Malacosoma disstria* (Roland & Kaupp 1995), but Peltonen & Heliövaara (1999) found no edge effect in predation for bark beetles. Actively avoiding edges to escape predation pressure has been demonstrated most convincingly for mammals (Bowers & Dooley 1993, Jacob & Brown 2000, Wahungu et al. 2001, but see Morris 1997), with some evidence for amphibians (Schlaepfer & Gavin 2001). Birds show little evidence of avoiding predation pressure at edges, and some species may be unable to assess risk accurately (Gates & Gysel 1978, Schlaepfer et al. 2002, Battin 2004).

Predation on plants (herbivory and seed predation) is also well documented, with many studies finding higher predation levels at the edge (e.g., Restrepo & Vargas 1999, Roach et al. 2001, Donoso et al. 2003, Tallmon et al. 2003). For example, higher abundances of white-footed mice (*Peromyscus leucopus*) at forest-clearcut edges lead to higher seed predation rates for *Trillium ovatum*, an understory herb, decreasing recruitment and thus reducing population size near edges (Jules & Rathcke 1999, Tallmon et al. 2003). Other studies have documented the opposite pattern, showing that some herbivores avoid edges, leading to reduced seed predation rates (Ostfeld et al. 1997, Manson et al. 2001, Nickel et al. 2003).

Competitive interactions and mutualisms can also influence the distribution of organisms near edges, but empirical studies are relatively rare. Morgan (1998) found no evidence for a competitive interaction between native and exotic plants species. In contrast, Argentine ants (*Linepithema humile*) appear to outcompete the local, native ant species at some edges (Suarez et al. 1998). The noisy miner bird (*Manorina melanoecephala*) inhabits open areas and adjacent forest edges and drives many forest bird species away from the edge (Piper & Catterall 2003). In theory, edges may even reverse competitive interactions (an inferior competitor becomes the superior competitor) on the basis of the edge's permeability and of the difference in quality between adjacent patches (Cantrell et al. 1998), but there is no empirical evidence for this. Most examples of edge-related mutualisms involve animal-mediated pollination and seed dispersal. For instance, trillium recruitment is decreased near forest-clearcut edges because of lower pollination rates, which may be the result of lower pollinator abundance at edges (Jules & Rathcke 1999). The ecology of animal seed-dispersers also influences plant colonization rates and dispersal distances on the basis of the animal's movement rates (Brunet & von Oheimb 1998, Ingle 2003).

Summary

Our model presents four mechanisms (ecological flows, access, resource mapping, and species interactions) that capture most dynamics driving edge responses

(Figure 3). Whereas most studies investigate only one type of mechanistic pathway, our model clearly illustrates how edge effects may arise through multiple pathways. These different mechanisms may interact in complex ways to influence an individual species' distribution and, ultimately, community structure at an edge (Figure 3). A single edge effect may create a cascade of edge effects in a wide range of organisms (Wiens et al. 1985). For instance, alterations in light levels near an edge may increase the abundance of a plant that an herbivorous insect subsequently maps onto. This may cause a decrease in that insect's competitors and/or an increase in local predator densities. This example illustrates the potential pitfalls of using correlational studies to ascertain the actual mechanism driving observed abundance patterns. When two factors change concordantly with respect to the edge, one is often interpreted as being the mechanism for the other, when this may not be the case.

Without manipulating potential pathways, it is difficult to conclusively identify the mechanism most directly responsible for an observed edge response. However, the distribution of resources, as well as species interactions, are identified as the major drivers underlying edge responses (Figure 3). Therefore, one way to avoid spurious conclusions that may result from correlational studies is to know which resources and interactions are most important in driving the abundance patterns of each study organism. Studies of edge effects in which the variables that drive organism abundance are assessed independently from, as well as in association with, edges are much more powerful than strictly correlational studies (e.g., Ross et al. 1997, Kristan et al. 2003), but they are rare. Another way to avoid spurious conclusions is to have a priori predictions for the expected response of each organism at each edge type. We next review a predictive model based largely on the concepts and mechanisms illustrated in Figure 3 and show how it can make sense of patterns and variability reported in the edge literature.

A PREDICTIVE MODEL OF EDGE RESPONSES

Although the mechanistic model presented earlier (Figure 3) offers some clues to the conditions that lead to positive, negative, and neutral responses for a particular species at a particular edge type, it is not specifically predictive. Until recently (Brand 2004, Ries & Sisk 2004), no models had been presented that allow a researcher to predict changes in abundance near edges. Brand (2004) presents models that are specific to birds at forest edges, which we review later. Below, we focus on a more general model that predicts changes in abundance near edges for any species in any landscape (Ries & Sisk 2004). This predictive model is a simplification of the mechanisms illustrated in Figure 3 and is based primarily on resource distribution (Figure 4).

Predictions from this model (Figure 4) are based on relative habitat quality of adjacent patches and the distribution of resources within and between each patch (Ries & Sisk 2004). Habitat quality is defined by the relative availability of

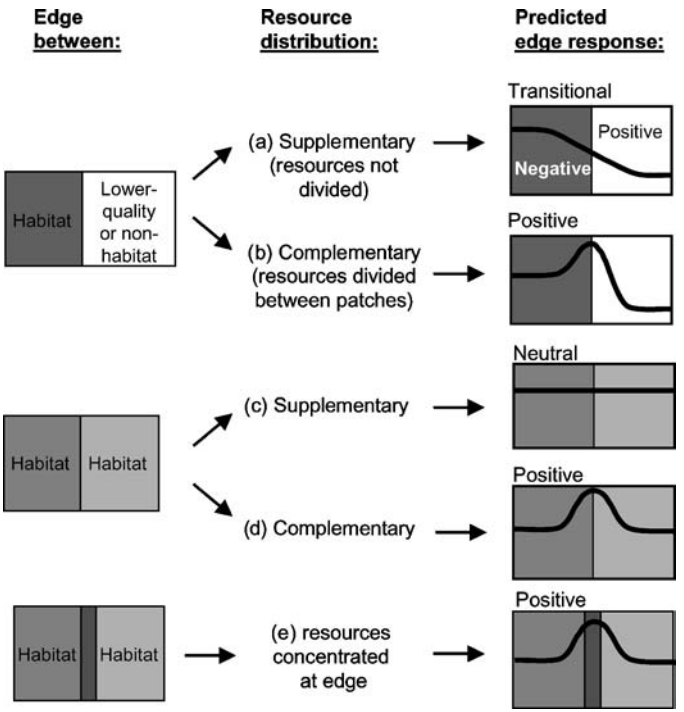

Figure 4 A predictive model of edge effects. This model is largely based on the mechanisms described in Figure 3. Edges are defined as the boundaries between patches, and patches are classified as habitat when they contain at least one resource, as nonhabitat when they contain no resources, and as lower-quality habitat when they contain fewer resources than the adjacent patch. When habitat borders nonhabitat or lower-quality habitat, where any available resources are (*a*) supplementary (the same) to those in the higher-quality patch, a transitional response is predicted. If there are resources in the lower-quality patch that are (*b*) complementary (different), then a positive edge response is predicted. When both patches contain resources, edge response predictions are based on whether the resources are (*c*) supplementary, which leads to a predicted neutral response, or (*d*) complementary in each patch, which leads to a positive prediction. When resources are (*e*) concentrated along the edge, a positive response is predicted. Reprinted with permission from Ries & Sisk (2004).

resources between the two patches. Patches are considered of lower quality when they contain fewer resources compared with the adjacent patch and nonhabitat when they contain no resources. Where organisms occur near nonhabitat or lower-quality patches, with supplementary resources (those that offer nothing different), organisms are predicted to decrease in abundance within higher-quality habitat near edges, although they may still spill over into the adjacent patch (Figure 4*a*).

This spillover is due to flows of materials between patches (Figure 3) that tend to make edges more similar to adjacent patches and cause a gradual transition in habitat quality onto which organisms may map (Lidicker 1999). In contrast, if the lower-quality habitat contains resources that are complementary (different), then a positive response is predicted on both sides of the edge (Figure 4*b*) because access to all resources is increased near edges (Figure 3). When two adjacent patches contain relatively equal amounts of resources, no response is predicted when resources are supplementary (Figure 4*c*) because being near the edge confers no additional access to resources. Again, complementary resource distribution leads to a predicted increase near edges (Figure 4*d*) owing to increased access (Figure 3). Finally, if resources are concentrated along the edge, organisms may map onto the increase of their resources near edges (Figure 3) and are therefore predicted to increase (Figure 4*e*). One important implication of this model is that all species are predicted to show positive, neutral, and negative edge responses, depending on the edge type encountered. This may explain much of the inter- and intraspecific variability reported in the edge literature.

A Test of the Model on Several Taxa

To evaluate the general applicability of this edge response model, we compared predictions with observed responses for four taxa: birds, butterflies, mammals, and plants. Outcomes are divided into cases in which the model is correct and in which it is incorrect; however, we further divided incorrect outcomes into two distinct cases. We classified cases in which the model failed to predict a significant positive or negative edge response as a "wrong" prediction and cases in which the model predicted a positive or negative edge response, but no response was found as a "neutral" outcome (Figure 5*a*). This distinction allows separate evaluation of the factors that may have led to unpredicted neutral responses versus unpredicted positive and negative responses, outcomes that may have different underlying causes. In addition, neutral outcomes, although still incorrect, may have causes (e.g., lack of statistical power) that do not necessarily conflict with the underlying framework of the model.

Two tests of this edge response model have already been carried out. On the basis of a review of the bird literature (Ries & Sisk 2004), the model correctly predicted the direction of 83% of edge responses observed for more than 50 avian species at edges between forests and open habitat (Figure 5*b*). An intensive field study testing the predictions of the model was carried out for 15 butterfly species at 12 edge types (Ries 2003). The model performed well in all but one habitat type (which exhibited a high degree of internal heterogeneity). In the other four habitats investigated, when positive or negative predictions were made, observed edge responses were in the predicted direction 75% of the time (Figure 5*c*).

To determine how well the model performs for other taxa, we conducted a test for plants and mammals using our database of 263 papers (reptiles and amphibians

(a) Analysis of model performance

Prediction	Observation -	0	+
-	Correct	Neutral	Wrong
0	Wrong	Correct	Wrong
+	Wrong	Neutral	Correct

(b) Birds

Pred	Observation -	0	+
-	11	18	4
0/+	0	7	5
+	0	3	9

(c) Butterflies

Pred	Observation -	0	+
-	19	55	5
0	2	46	7
+	8	61	21

(d) Mammals

Pred	Observation -	0	+
-	7	0	4
0/+	1	1	9
+	0	0	3

(e) Plants

Pred	Observation -	0	+
-	6	1	1
0	0	0	0
+	0	0	4

Figure 5 Analysis of the performance of the edge effect model (Figure 4). (*a*) Outcomes are separated into cases in which the model was correct and incorrect. Incorrect outcomes are further separated into two separate cases in which an unpredicted neutral response was observed and cases in which wrong positive or negative responses were observed. Results are presented for tests of the model on four taxa. (*b*) Bird results are from Ries & Sisk (2004). (*c*) Butterfly results are from Ries (2003). (*d*) Mammal and (*e*) plant results are from a review of the literature, and details for these tallies are given in Appendix 1b. (The Appendix is included as Supplemental Material. Follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org.) Note that for birds and mammals, we lacked information to differentiate between positive and neutral predictions in some cases, so outcomes were identified as correct if either observation was recorded. Outcomes for which model predictions were correct are shaded in gray.

were not included because too few studies were available). This test allowed a determination of how generally applicable this model is across a wide variety of taxa and edge types. For both plants and mammals, we predicted a negative edge response when abundances were measured in the superior habitat and a positive response in lower-quality or nonhabitat (Figure 4*a*). Information on resource distribution (complementary versus supplementary) was rarely included, so for mammals, when a species was associated with both habitat types, either a neutral

or positive (but not negative) response was predicted (see Figure 4*c*,*d*). This distinction was not necessary for plants because sessile organisms cannot generally gain access to resources in two separate patches. Observed edge responses were in the direction predicted by the model in 83% of cases for mammals (Figure 5*d*) and 91% for plants (Figure 5*e*). Papers used to test the model for mammals and plants are detailed in Appendix 1b (see Supplemental Material).

It is clear from these four tests (Figure 5*b*–*e*) that when edge responses are observed, they are largely predictable, even for different species at different edge types. Negative edge responses are due to individuals avoiding edges of low-quality habitat, and positive responses result when organisms gain access to resources either in adjacent patches or near edges. Some variability clearly remains unexplained; yet by using this model to isolate unpredicted responses, researchers can more easily focus on the remaining variability and attempt to account for it. Except for birds at forest edges (see below), there are no alternative predictive models with which to compare the performance of this model.

Accounting for Remaining Variation

For mammals, most unexplained variation comes from observing positive responses when negative ones were predicted (Figure 5*d*). This anomaly is potentially due to a lack of information on resource distribution, because a positive response would be predicted if complementary resources were known to occur in the less-preferred patch (Figure 4*b*) or if resources were concentrated along the edge (Figure 4*e*). Although resource distribution (either complementary, supplementary, or concentrated along the edge) is critical to the generation of more precise model predictions, this information is never as widely available as basic information on habitat associations. We therefore suggest that the relative distribution of critical resources on both sides of the edge should become standard information reported in edge studies.

For birds (Figure 5*b*) and butterflies (Figure 5*c*), most unexplained variation came from observing unpredicted neutral responses rather than unpredicted positive or negative "wrong" responses. One potential cause of these unpredicted neutral responses is that some species may be particularly insensitive to edges (Wiens et al. 1985, Lidicker 1999). Many species are often labeled as edge species, but this is likely due to a historical focus on a single edge type (forest edges). This labeling is especially true for birds, which are routinely classified as edge or interior species, as if such behaviors were consistent across all habitats and edge types. Although these classifications are under increasing challenge (Baker et al. 2002, Imbeau et al. 2003), they are still commonly used. Because the edge response model predicts that all species will show neutral responses at some edge types (Figure 4*c*), to gauge edge sensitivity accurately researchers must separate predicted neutral responses from unpredicted neutral responses. Only species that consistently fail to show edge responses where they are predicted should be considered edge insensitive. Currently, rigorous classification of any species as edge

sensitive or insensitive is difficult. However, it would be useful to determine if some species are intrinsically less sensitive to habitat edges and, if so, if any life-history or ecological characteristics are associated with that insensitivity. Several characteristics, such as body size, mobility, and vulnerability to predation, have been suggested to influence overall sensitivity (Wiens et al. 1985, Lidicker 1999), although little evidence exists to substantiate these ideas.

Brand (2004) studied the ecological and life-history characteristics associated with edge responses in forest birds. In addition to habitat utilization characteristics (that closely mirror the predictions illustrated in Figure 4*a*,*c*), species are more likely to exhibit negative responses to forest-open edges if they require mesic conditions, have smaller body sizes, are less ecologically plastic, and have longer incubation and nestling periods (Brand 2004). Likewise, species are more likely to exhibit positive responses to the same forest edges if they nest in shrubs, have open cup nests, and are more ecologically plastic (Brand 2004). In the only other study of traits associated with edge sensitivity, Ries (2003) found that butterflies are more sensitive to edges if they are more vulnerable to predation and lighter in color (making them potentially more sensitive to microclimatic variation).

Another cause of unpredicted neutral responses is that most edge studies have low replication and therefore little power to detect any but the strongest responses (Murcia 1995). This problem is exacerbated by any ecological factor that interacts to weaken edge responses, a topic we explore in the following section. Finally, the predictive edge response model illustrated in Figure 4 is a necessary simplification of the complex pathways and different mechanisms presented in Figure 3. When unpredicted responses occur, it is useful to return to that underlying mechanistic framework and determine if critical resources were not considered, other species interactions were occurring, or complex pathways were not captured by the simplifying assumptions of this predictive model.

INTERACTIONS AFFECTING EDGE RESPONSES

Several studies have explored how a suite of ecological factors influence observed edge responses, and these studies allow insight into some of the unexplained variation described above. We review the four factors that have received the most attention: edge orientation, temporal effects, habitat fragmentation, and edge contrast. To explore these factors rigorously, we reviewed studies that measured edge responses for the same species at the same (or comparable) edge types while varying one of the above four factors. We then determined the percentage of times each factor influenced edge responses to cause the following four outcomes: (*a*) no interaction with edge responses; (*b*) expression, defined as a unidirectional edge response observed in some situations but not others; (*c*) strength, defined as changes in the magnitude of the effect or the distance it penetrates into the patch; or (*d*) direction, defined as an edge response switching direction from positive to negative or vice versa (see Figure 6).

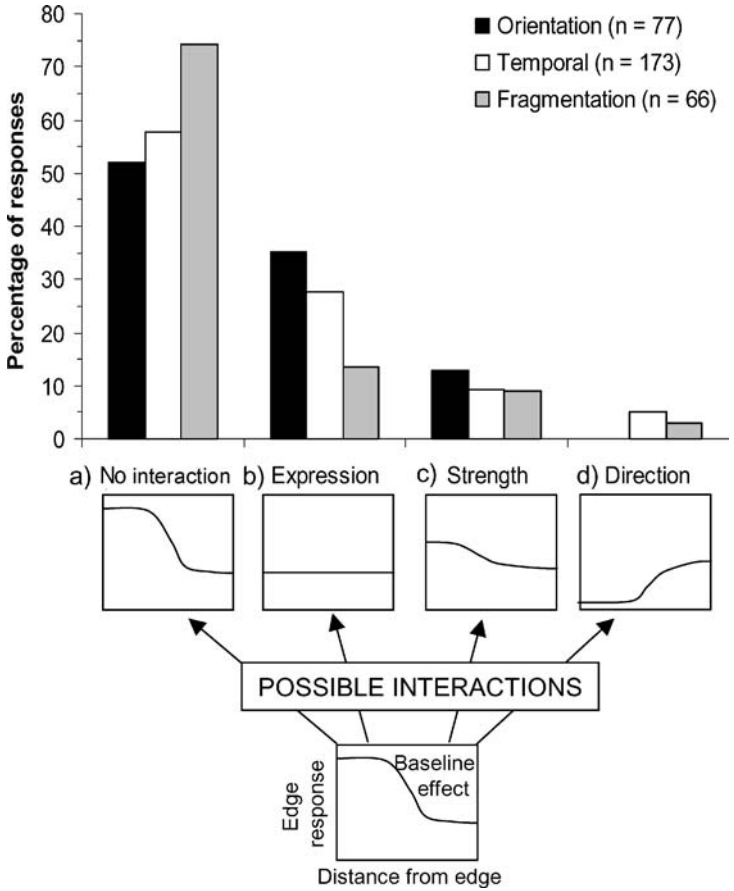

Figure 6 The influence of ecological factors that may interact to influence observed edge responses. Edge responses were compared within the same study for interactions on the basis of different orientations within the landscape, different temporal effects (daily, monthly, seasonally, or annually), and different levels of fragmentation. Outcomes of these comparisons fell into four classes. The ecological influences of orientation, time, or fragmentation either had (*a*) no interaction with observed edge responses, (*b*) caused an observed edge response not to be expressed, (*c*) changed the strength of an observed edge response, or (*d*) caused the observed edge response to change direction. The figure shows the percentage of times each outcome was observed. Details for each study are given in Appendix 1c.

Edge Orientation

The mechanistic model in Figure 3 indicates that the flow of energy is one of the fundamental drivers of edge responses. Because solar radiation is a major factor influencing the movement of energy, edges in different positions relative to the

sun are likely to experience different rates, but not directions, of energetic flows (Matlack 1993, Dignan & Bren 2003b). Several studies have demonstrated that edge orientation can impact the strength or expression, but never the direction, of edge responses (Figure 6). Because edge orientation is rarely controlled for (Murcia 1995), it may be one cause of the unpredicted neutral responses reported earlier for the test of the edge response model, but not of the unpredicted positive and negative "wrong" responses (Figure 5).

If differential permeability to abiotic flows is the primary mechanism causing edge responses to weaken based on edge orientation, then we might expect two patterns. The first expected pattern is that orientation effects will be different in different latitudes. Specifically, in the northern temperate zones, south-oriented forest edges bordering open habitat should exhibit stronger edge effects (because of increased exposure to sunlight) than north-oriented edges. The converse should be true in the southern hemisphere (Kapos 1989, Young & Mitchell 1994), and little difference should be found in the tropics. These predictions may vary for other edge types, but only data on forest edges have been reported. There is strong support for the hypothesis that south-facing forest edges exhibit stronger edge responses in the northern temperate zone. When there were significant interactions in the northern hemisphere, edge responses were stronger or were expressed only at south-facing edges 42% of the time, compared with 3% at north-facing edges ($n = 67$). In the remaining cases, there was no interaction (Appendix 1c). Studies in the tropics and southern temperate zones were too rare to allow us to determine if patterns in those regions matched expectations.

The second expected pattern is that orientation will have a stronger influence on microclimatic patterns than on plant patterns and that the importance of orientation might continue to decrease through successively higher trophic levels. Orientation had a measurable effect on abiotic responses 63% of the time ($n = 19$), compared with only 42% of the time for plants ($n = 50$) (Appendix 1c), suggesting that damping may be occurring. Currently, there are too few studies on orientation effects on animals to determine if this damping effect occurs at higher trophic levels.

Temporal Effects

Temporal effects on edge responses have been investigated at a variety of scales, including time of day (Meyer et al. 2001), season (Young & Mitchell 1994), and year (Chalfoun et al. 2002a). Although these effects, particularly year effects, are often considered nuisance parameters, understanding their cause could help explain much of the observed variability in edge responses (Figure 6). Time most likely affects edge responses because of temporal patterns in resource distribution or use (Manson & Stiles 1998) that could vary either seasonally (Noss 1991, Young & Mitchell 1994) or throughout the day (Meyer et al. 2001). Predictable seasonal or daily change in resource use or distribution can be incorporated into the predictions of the edge response model (Figure 4) by stratifying predictions by season or time of day. Depending on how resource use or distribution changes temporally, it is

even possible that the direction of an edge response could reverse, although these types of changes are rare (Figure 6*d*). Information on daily or seasonal changes in resource use or distribution are usually not reported, making this prediction difficult to test explicitly from the current literature. Year effects may also be driven by changes in resource distribution but are more difficult to predict than daily or seasonal effects because they likely originate from stochastic events, potentially driven by broad climatic patterns. Other temporal effects may originate from lag times in species responses, especially in sessile organisms with long generation times (e.g., Rose & Fairweather 1997) or from more gradual changes as the quality of the edge or adjacent patch changes through time.

Habitat Fragmentation

Fragmentation effects, which include patch size, isolation, and landscape composition, had the least effect on measured edge responses (Figure 6), although this pattern is strongly influenced by the results of one study (Moen & Jonsson 2003). When researchers did detect an interaction, the responses measured in one type of landscape were most commonly not expressed in another (Figure 6*b*). For example, brown-headed cowbirds are more likely to express edge responses in highly fragmented landscapes (Donovan et al. 1997), whereas black-tailed deer (*Odocoileus hemionus columbianus*) showed the opposite effect, with edge responses more likely when landscapes were less fragmented (Kremsater & Bunnell 1992). Many potential mechanisms are responsible for fragmentation influences on edge effects, and those mechanisms may be situation specific, making predictions difficult. Therefore, placing fragmentation interactions into a predictive framework may prove to be more difficult than for other factors discussed in this review.

Edge Contrast

Edge contrast may influence edge effects, and researchers generally assume that responses will be weaker near "soft" (low-contrast) edges than near "hard" (high-contrast) ones (Stamps et al. 1987, Duelli et al. 1990). Two main factors underlie differences in edge contrast: (*a*) differences in mean vegetation height between adjacent patches forming the edge, and (*b*) different vegetation densities within the same edge type. For both factors, differences in edge responses are likely due to differences in the permeability of the edge, resulting in different rates of ecological flows (Figure 3). Therefore, when differences in edge responses are due to edge contrast, the strength of the response is more likely to be affected than its direction. Few studies allow rigorous comparisons of edge contrast (so this factor is not included in Figure 6); however, results are similar to those presented earlier in that when a significant interaction is found, strength or expression is affected, but rarely direction.

The influence of edge contrast based on relative vegetation height is rarely rigorously explored because most studies do not control for differences in the

relative qualities of the adjacent patches. This shortcoming is critical, because differences in adjacent habitat qualities are predicted to influence the strength of edge responses (Ries & Sisk 2004), and quality is often correlated with the degree of edge contrast, making these two factors particularly difficult to disentangle. Studies that have effectively controlled for habitat quality while varying edge contrast show mixed results. Fletcher & Koford (2003) found that grassland-dependent bobolinks (*Dolichonyx oryzivorus*) exhibited stronger edge avoidance near woodland edges (high contrast) than near rowcrop edges (low contrast), even though both constitute nonhabitat. Ries & Debinski (2001) found that the likelihood of a prairie endemic butterfly turning to avoid edges was stronger at high-contrast nonprairie edges than at low-contrast edges. In contrast, Ries (2003) found that edge contrast had no effect on the edge response of butterflies at several different kinds of riparian habitat edges.

The second type of edge contrast study, in which edge type is the same but vegetation structure in the focal habitat varies, is also rare but has received more rigorous treatment because the edges have been experimentally manipulated, a rarity in the edge literature. In the first example, the understory structure of a deciduous forest near an open edge was experimentally thinned. The change in vegetation density influenced whether edge responses were expressed for nutrient concentrations (Weathers et al. 2001) and rates of seedling herbivory by voles and deer (Cadenasso & Pickett 2000). The strength of edge responses varied for seed dispersal (Cadenasso & Pickett 2001). Likewise, Didham & Lawton (1999) compared relatively "open" and "closed" edges in experimentally created forest fragments in Brazil and found that edge responses were not expressed in closed-structure edges for canopy density, litter depth, or biomass, whereas edge responses changed direction for litter moisture.

Summary

The ecological factors examined rarely showed a significant interaction with edge responses (Figure 6*a*), but when they did, responses observed in one situation were either not expressed in another (Figure 6*b*) or the strength of the edge effect was modified (Figure 6*c*). In some cases, edge responses that were not observed may represent cases in which response strength was really affected but a lack of statistical power limited the ability to detect weaker patterns. The design of most edge studies, which often have low replication, few distance categories, and little penetration into patches, limits the detection of more subtle changes in edge response strength. In contrast, most edge studies are designed to capture differences in response direction, yet these cases are by far the least common outcome (Figure 6*d*). This fact suggests that changes in edge response direction for the same variable at the same edge type are rare occurrences. This pattern is encouraging and contrasts with the common conception that edge responses are intractably variable. It also suggests that, when edge responses are documented for specific species at specific edge types, managers can use this information as

a generally reliable characteristic, with unforeseen shifts in the direction of edge responses unlikely to limit conservation strategies. Finally, interactions are often based on factors that are consistent with the models presented (Figures 3 and 4) and can therefore be either incorporated directly into predictions generated from the edge response model (Figure 4) or understood within the framework of our mechanistic model (Figure 3). Together, these models provide a tractable approach for understanding variability in edge responses.

EXTRAPOLATING EDGE RESPONSES TO LARGER SCALES

The main rationale cited for carrying out most edge studies is to understand better how landscape structure, usually fragmentation, influences the distribution and abundance of organisms. Although much progress has been made in describing how edges influence distributions at local scales, progress has been more limited in extrapolating measured responses to larger scales. This limited progress is unfortunate because knowledge of edge responses can contribute meaningfully to management and conservation strategies, particularly in landscapes undergoing rapid change (Sisk & Haddad 2002, Sisk et al. 2002, Battin & Sisk 2003). Few studies have tested how information on edge responses can be used to improve the understanding of distributions at larger scales (but see Temple 1986, Sisk et al. 1997, Haddad & Baum 1999).

Studies that are designed specifically to determine the role of edges as mechanisms underlying fragmentation-related patterns often demonstrate a direct link (Rosenberg & Raphael 1986, Roland 1993, Burke & Nol 1998, Didham et al. 1998, Bolger et al. 2000, Davies et al. 2001, Fletcher & Koford 2002). Furthermore, a formal meta-analysis of patch-size effects shows that species that avoid edges show increased densities in larger patches, and edge-attracted species show the opposite effect, whereas species that do not respond to edges show weak or no patch-size effects (Bender et al. 1998). This result suggests that edge responses are one of the main factors driving area sensitivity. Despite the obvious connection, three factors have limited researchers' ability to extrapolate edge responses to larger landscapes: (*a*) a lack of models and the software tools to implement them, (*b*) an incomplete knowledge of how deeply into patches edge effects extend, and (*c*) a poor understanding of how responses are influenced by the presence of multiple edges. We end this section with a brief discussion of how "scaling up" edge responses may help inform our understanding of population and community dynamics.

Models and Software Tools

Two primary models are used for "scaling up" edge responses to real landscapes: the core area model (Temple 1986, Laurance & Yensen 1991) and the effective area model (Sisk & Margules 1993, Sisk et al. 1997). Core area models use an estimated distance of edge influence to determine the amount of habitat in a patch that is not affected by edges (the core area). This model constitutes a significant

advance in that it allows researchers to consider the portion of a landscape that is thought to be free of edge influences, and this model is often used when considering reserve designs (Temple & Cary 1988, Laurance 1991, Zipperer 1993, Ohman & Erikson 1998). Several software packages have the ability to measure the amount of core area in a landscape, facilitating the use of this approach. However, core area models have limited utility for species exhibiting variable responses to edges or in severely fragmented landscapes where most core habitat has already disappeared. The effective area model extends the core area approach by describing density (or other parameters) as a function of distance from edge, allowing researchers to generate quantitative predictions of distributions throughout an entire landscape. Furthermore, it allows researchers to specify different edge responses for each species at each unique edge type (Sisk et al. 1997, Sisk & Haddad 2002), thereby reflecting the complexity that exists in real landscapes (see Figure 1*b*). However, this model's use is currently limited by a lack of data for parameterization. Furthermore, software, although available, is at an early stage of development (Sisk et al. 2002).

Neither of the above models can incorporate variable edge responses based on landscape-level interactions, including edge orientation, patch size, or fragmentation effects (but see Zheng & Chen 2000). In the previous section, we demonstrated that these factors can interact to modify edge responses but that only strength or expression are generally affected, rarely the direction of the response (Figure 6). Edge responses are thus likely to manifest at larger scales in a predictable direction (Kolbe & Janzen 2002), but resulting magnitudes may be dampened depending on the extent to which orientation and landscape structure interact either to weaken edge responses or limit their expression.

Depth of Edge Influence

For both core area and effective area models, researchers must know the distance that edge effects extend into habitat patches. This value, often referred to as the depth of edge influence (DEI), is critical for determining the scale at which edge responses operate in larger landscapes (Laurance 2000). Although DEI values are reported for many edge responses, only recently have statistical techniques been suggested to allow for a rigorous determination of DEI (Fraver 1994, Cadenasso et al. 1997, Laurance et al. 1998, Mancke & Gavin 2000, Brand & George 2001, Harper & MacDonald 2001, Toms & Lesperance 2003). In many studies, DEI is determined by "visual inspection," and these numbers are likely influenced by study design (i.e., the length of survey transects and the number of distance categories). Without controlling for the statistical rigor of each study, abiotic and plant responses are generally reported to extend up to 50 m into patches, invertebrate responses up to 100 m, and bird responses 50–200 m (Appendix 1d). Examples of deeper DEIs exist for all classes, and Laurance (2000) suggested that some edge effects might occur over the scale of kilometers, yet most studies are not designed to capture effects at this scale. As empirical studies employ more rigorous designs

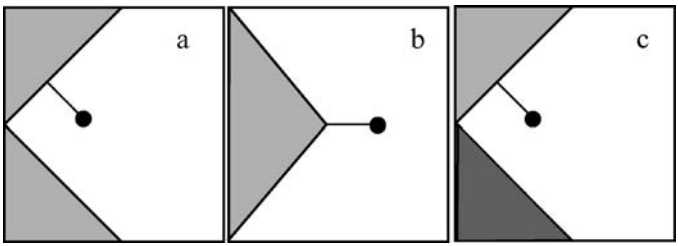

Figure 7 Complex and multiple edge effects. In most published studies, the influence of the edge is described for a point on the basis of the distance from that point to the nearest edge (shown by the dot and line), which is the same for all three panels in this figure (*a*, *b*, *c*). However, the type and strength of edge influence is likely to be different for each situation. Even at the same edge type (*a*, *b*), the geometry of the patch shape is likely to exhibit complex effects that cause edge influences to be either (*a*) greater or (*b*) lesser on points equidistant from the closest edge. A further complication that has received no empirical treatment is the convergence of multiple edge types at one point (*c*).

and statistical techniques, estimates of DEI can be more easily compared and used in landscape-level extrapolations.

Multiple Edge Effects

Another critical issue when extrapolating edge responses to landscapes is that most empirical research on edge effects has ignored the cumulative effect of being near more than one edge. Most studies (and models) use the linear distance to the closest edge as the main explanatory variable (Figure 7), and researchers generally avoid placing plots near corners or other converging edge types to limit their potential influence. However, complex patch geometry and the convergence of multiple edge types are dominant features of all real landscapes (see Figure 1*b*). If edge responses are different near multiple edges, then that factor should be incorporated into any model that extrapolates edge responses to complex landscapes. Multiple edge effects arising from complex patch geometry (Figure 7*a*,*b*) are poorly understood, yet they almost certainly influence the strength of edge effects by influencing both the magnitude and the depth of edge influence (Chen et al. 1995). For example, bobolinks exhibit a greater reduction in their probability of occurrence in plots located near corners compared with straight edges (Fletcher 2003). A further complication of multiple edge effects can arise when different edge types converge (Figure 7*c*), potentially causing complex edge responses on the basis of the relative influence of each adjacent habitat type (Fernandez et al. 2002). We know of no empirical studies that measure how edge responses are affected by the convergence of multiple habitat types. Mathematical approaches to deal with these issues have been suggested (Malcolm 1994, Mancke & Gavin

2000, Zheng & Chen 2000, Fernandez et al. 2002, Fletcher 2003), but the lack of empirical treatment severely limits our ability to understand how edge responses manifest in real landscapes.

Population and Community Consequences

Edge responses can also "scale up" to influence long-term population dynamics and community structure. The parameters that ultimately determine distributions (birth, death, immigration and emigration rates) are rarely modeled with respect to edges, which makes determining a cumulative influence of edges on population dynamics difficult. Edge effects may not have strong implications on population-level parameters, such as population growth rates, if the effect is weak or the response variable is not a limiting factor in population regulation. For example, Flaspohler et al. (2001) examined whether edge effects could affect population growth rates of ovenbirds. Although nest predation increased near edges, clutch size was higher, thereby offsetting predation and causing estimates of population growth rates to be similar for edge and interior habitats (see also Harris & Reed 2002). Also, the degree to which edges are important depends on the strength of the response and the relative amount of edge in a landscape (With & King 2001, Fletcher 2003). For these reasons, knowledge of edge responses may, in some cases, have limited utility in understanding population dynamics.

Although we have focused on individual species' responses to edges, our mechanistic model shows that changes in individual species' distributions ultimately culminate in an altered community at the edge (Figure 3). However, a framework for predicting community-level responses to habitat edges currently does not exist. Many studies have measured community changes near edges, with increases in species diversity the most common result (Table 1), but the causes and implications of changes in diversity near edges remain unclear. Increased diversity near edges could arise from an additive effect of species using each habitat type, increases of species using novel edge habitat, or some other emergent property. If increased diversity near edges is indeed a common and widespread pattern, the implications have received little exploration.

Summary

Despite decades of research describing how a suite of organisms respond to habitat edges, the tools to extrapolate edge responses to the landscape scale effectively and the specific data required to do so remain limited. Most studies are not designed to allow even the most basic models to be rigorously parameterized. Depth of edge influence is rarely quantified in a rigorous way, and the influence of multiple, complex edge effects has, for the most part, been ignored. This is unfortunate because understanding and predicting edge responses are clearly keys to understanding the impacts of fragmentation and other landscape-level changes. A recent review of the fragmentation literature (Fahrig 2003) admonished researchers to approach the study of fragmentation in a way that allows the impacts of habitat loss to be clearly

separated from those of habitat structure. Understanding how edges impact patch quality is clearly one approach to meeting that important goal. A greater understanding of how edge responses influence population and community dynamics is also needed. Much work remains to be done to develop the knowledge and tools to accomplish this. Until these questions are more rigorously addressed, our ability to use edge response data to inform conservation and management issues remains limited.

CONCLUSIONS

Our review of the edge literature shows that the mechanisms underlying edge responses have been well described over several decades of research. The two models we present provide tools to make sense of a highly descriptive and variable literature. Our mechanistic model (Figure 3) illustrates four fundamental mechanisms underlying edge responses: ecological flows, access to spatially separated resources, resource mapping, and species interactions. These mechanisms form the basis of a general, predictive model of edge responses (Figure 4) that can be used for any species in any landscape. Our review of an extensive literature shows that edge responses, when observed, are generally predictable and consistent when species and edge type are held constant. This pattern contrasts with the generally held view that edge responses are largely idiosyncratic and based on disparate ecological phenomena. These models capture most variation, and additional variation can be explored by allowing researchers to focus on unpredicted outcomes. We identify several factors, including intrinsic sensitivity to edges, edge orientation, edge contrast, fragmentation effects, temporal shifts in resource distribution or use, and study design, that may influence observed edge responses. Finally, although many of the patterns and much of the variability in the current edge literature can be accounted for with these models, the tools necessary to extrapolate those responses to larger landscapes or to use them to understand population dynamics and community patterns have received less development, limiting our ability to use this information to inform conservation and management decisions in real, dynamic landscapes. We hope that this synthesis stimulates future research by allowing studies to be carried out under a theoretical, predictive framework. Edge responses are a key component in furthering our understanding of landscape-level dynamics, and their study continues to hold great promise in contributing even more to our growing understanding of how the spatial patterning of landscapes influences the abundance and distribution of organisms.

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(a) A simplified view of edges between habitat and non-habitat in a "fragmented" landscape

(b) Edges are more complex when the same landscape is viewed in the context of a mosaic of different patches

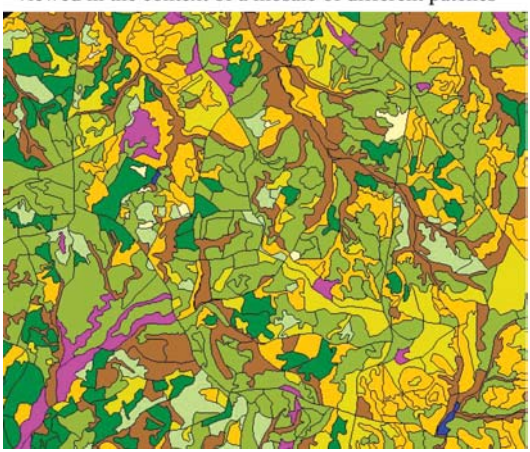

Figure 1 Dark green patches show the distribution of old-growth long-leaf pine (*Pinus pilustrus*) on a section of Ft. Benning in Georgia, USA. These pine stands are habitat for the red-cockaded woodpecker (*Picoides borealis*), an endangered species restricted to the Southeast. In the top panel (*a*), habitat is illustrated in a classic "fragmentation" context, where all patches are portrayed as either habitat (*dark green*) or nonhabitat (*white*). In fact, the surrounding landscape forms a complex mosaic (*b*) that has multiple influences on each patch. Lighter greens represent younger pine age classes, yellow patches are open or brushy habitat, brown represents hardwood stands, orange is mixed hardwood-pine stands, and purple is areas developed for military use. The influence of these different types of patches, experienced largely as "edge effects," can be as varied as the types of patches found within the landscape. Forest stand maps are used with permission of Ft. Benning.

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Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies

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Abstract

Reconstructing prairie habitat is one of the most promising techniques for conserving the imperiled prairie ecosystem and its associated organisms. However, the degree to which reconstructed prairies function like remnant prairies has not been fully examined. We evaluated the effect of restoration planting prescriptions, as well as vegetative quality on butterfly communities inhabiting prairie reconstructions in central Iowa, USA. Twelve isolated reconstructed prairies (small, surrounded by agriculture), 12 integrated reconstructions (planting units in a larger matrix of reconstructed and remnant prairies), and 12 remnant prairies were surveyed for butterfly and plant diversity, abundance and composition. Remnant prairies supported significantly higher richness and abundance of habitat-sensitive butterfly species. Butterfly richness on integrated reconstructions was intermediately positioned between remnant and isolated reconstructions. The best vegetative predictors of butterfly richness ($R^2 = 0.38$) and abundance ($R^2 = 0.13$) were the availability of nectar and the percent cover of litter (which is related to management issues such as time since burning). Most significantly, we found that the response of the butterfly community to vegetation in a reconstructed prairie is more complex than simply a response to vegetation diversity. Both management within the reconstruction and the landscape context around the reconstruction affect local patterns of butterflies species distribution and abundance. Integrated reconstructions develop richer butterfly communities than isolated reconstructions.
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Keywords: Prairie; Restoration; Butterflies; Reconstruction; Habitat isolation

1. Introduction

Arguably one of the fastest developing segments of conservation biology is the practice and theory of restoration ecology (Jordan et al., 1988; Hobbs and Norton, 1996; Packard and Mutel, 1997). Restoration ecology can be loosely defined as the process of repairing or recreating natural ecosystems that have been damaged by the actions of humans (Jackson et al., 1995). Ecological reconstruction is unique by having as a goal the recreation of destroyed ecosystems. From a conservation perspective, the recreation of a productive natural landscape is needed in areas of high anthropogenic influence and alteration (Jordan et al., 1988; Hobbs, 1993; Recher, 1993), such as the restoration of tallgrass prairie in the Midwestern USA. The tallgrass prairie is one of the most endangered ecosystems in the world. The state of Iowa supports only 0.1% of its historical millions of acres of prairie because of extensive conversion of land to agricultural uses (Smith, 1998). In light of this statistic, it is clear that by adding areas of natural vegetation, prairie reconstructions in Iowa will have a larger conservation impact than simply preserving the few, small isolated existing prairie remnants in isolation

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(Hobbs, 1993). As a result, several prairie restoration projects have been initiated in the last 15 years in a variety of situations throughout the state.

One of the most important challenges facing restoration practitioners and theorists is determining how to assess a restoration project's success or failure (Ewel, 1987; Harper, 1987; Westman, 1991; Saunders et al., 1993). Ideally, the goal of restoration and reconstruction is to restore the presence and interactions of floral, faunal and abiotic components (Hobbs, 1993; Jackson et al., 1995). Eventually, a reconstruction should not only look like, but also function like its remnant counterpart in terms of ecosystem processes and trophic interactions. Assessments of restoration projects often focus exclusively on basic measurements of the plant community (species richness, composition) but the importance of evaluating other elements of the ecosystem is being recognized, in particular the potential of the arthropod community to serve as indicators of ecosystem development (Erhardt and Thomas, 1991; Williams, 1993; Andersen and Sparling, 1997; Jansen, 1997; Wheater and Cullen, 1997; Bisevac and Majer, 1999).

Here, we examine how butterfly communities respond to prairie reconstructions in both isolated and integrated settings. Butterflies are a logical group for study because of their association with the plant community as important herbivores and pollinators (Scott, 1986; Hendrix and Kyhl, 2000). Adult butterflies are easy to sample and can serve as indicators of ecosystem health (Erhardt and Thomas, 1991; Kremen, 1992; Panzer et al., 1995; Holl, 1996; Hammond and Miller, 1998; Oostermeijer and van Swaay, 1998; Brown and Freitas, 2000; Pywell et al., 2004; Poyry et al., 2005). Lepidoptera (i.e., butterflies and skippers in this context) contain a large but not overwhelming number of species (50–60 species on Iowa prairies), exhibiting varying degrees of habitat specificity and disturbance sensitivity (Opler and Krizek, 1984; Scott, 1986; Panzer et al., 1995; Schlicht and Orwig, 1998). They are, therefore, very useful in assessing the reestablishment of trophic interactions in reconstructions of varying quality or similarity to remnants. Additionally, open areas and grasslands are important habitats for butterflies and several species that depend on grassland habitat in North America (e.g., *Speyeria idalia*, *Oarisma poweshiek*, *Hesperia dacotae*, *Hesperia ottoe*, *Coenonympha tullia*) are in decline (Schlicht and Orwig, 1998). Restoration may play a critical role in the survival of these and other prairie endemic butterflies (Orwig, 1990; Debinski and Kelly, 1998; Schlicht and Orwig, 1998).

For the purposes of this study, reconstructed prairie was defined as the recreation of a destroyed ecosystem, which in central Iowa most often meant the conversion of a crop field into prairie vegetation. We examined relationships between aspects of the vegetative community and the butterfly community to determine how closely butterfly richness, abundance and species composition were linked to shifts in quality (defined as similarity to remnants) of the restored plant community. We compared reconstructed prairies with several remnant prairies that served as reference communities (Aronson et al., 1995; Kondolf, 1995; White and Walker, 1997). There is evidence that remnant ecosystems, on average, have higher plant diversity (Wheater and Cullen, 1997; Brand and Dunn, 1998) and support a higher diversity of butterflies (Selser and Schramm, 1990; Panzer et al., 1995; Debinski and Babbit, 1997) then reconstructed prairies.

By examining plant composition in remnants versus reconstructions we were also assessing how variance in the plant community may influence the butterfly community. The reconstructions chosen ranged from standard wildlife plantings of only a few native prairie species, to reconstructions planted with over 200 native prairie species. Many assessments focus on the age of the restoration project as the primary variable in measuring whether success has been attained (van Aarde et al., 1996; Jansen, 1997; Brand and Dunn, 1998; Bisevac and Majer, 1999; Reay and Norton, 1999) but the original planting formula and subsequent management may be more significant in shaping the developmental trajectory of the restoration (MacMahon, 1987; Chambers et al., 1994; Wheater and Cullen, 1997; Bomar, 2001). Here we do not use reconstruction age as a variable, but rather assess vegetation variables directly in terms of their association with butterfly species richness and abundance patterns.

The questions addressed in this study are: (1) Do remnant prairies in central Iowa support a more diverse butterfly and plant community than reconstructed prairies? (2) Does butterfly diversity and abundance exhibit a positive trend as vegetative quality (defined as the level of similarity to remnant communities) on reconstructed prairies becomes higher? (3) With what prairie vegetative components are butterfly diversity and abundance most correlated? (4) How do isolated and integrated prairie reconstructions differ in their butterfly communities relative to prairie remnants?

2. Methods

2.1. Study area

We surveyed the butterfly and plant communities on 36 prairies, located in an approximately 65 mile radius of Ames in central Iowa (Fig. 1). All but two of these sites fall within the geological feature called the Des Moines lobe and thus have similar soil type and geological history. Twelve sites were native prairie remnants chosen as reference sites for comparison with 24 reconstructed prairies. All reconstructions were planted between 1991 and 1998 (4–11 years old). Twelve recon-

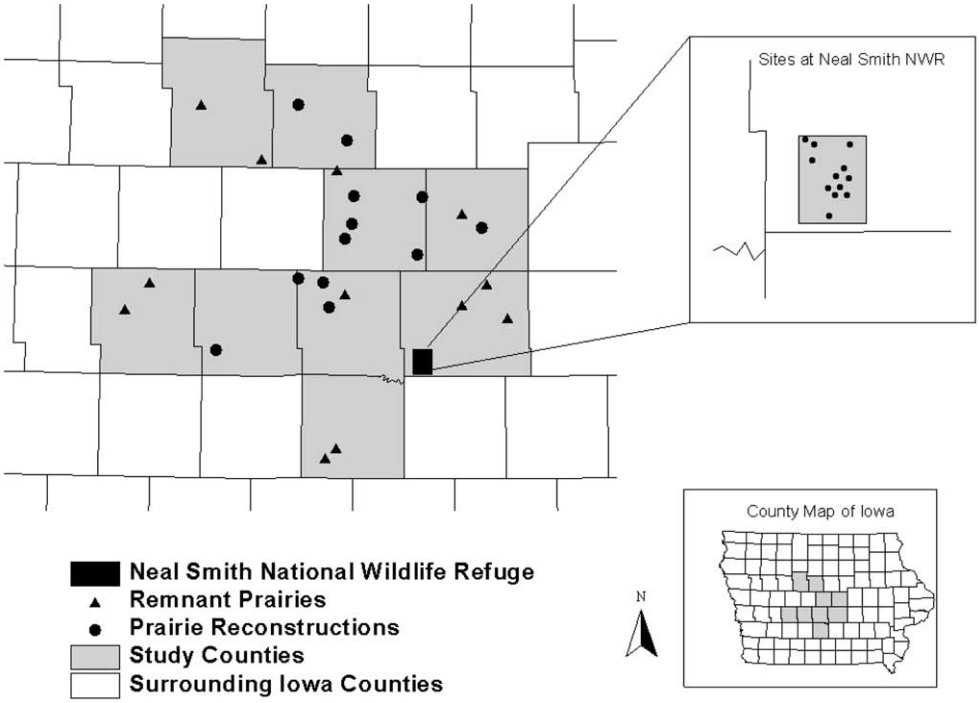

Fig. 1. Map of study areas showing approximate locations of reconstructed and remnant prairies in Central Iowa, USA. Insets show the context of the sites within Iowa and a closer view of the 12 reconstructed prairie sites at Neal Smith National Wildlife Refuge.

structed sites were units within a much larger reconstruction at Neal Smith National Wildlife Refuge (NWR) in Prairie City, Iowa (Fig. 1), and hereafter will be referred to as "integrated reconstructions." Neal Smith NWR encompasses 1250 hectares of reconstructed prairie on a total 2083 hectares of refuge property. The matrix for these sites was a combination of reconstructed prairie and small prairie remnants present on refuge property. Planting units used for our research were 310 m or more from a remnant prairie to limit direct spillover of the remnant's butterfly community onto the reconstructions. In addition, reconstructed sites within Neal Smith NWR were at least 200 m apart. Using the strictest sense of the definition, one might argue that the sites at Neal Smith National Wildlife Refuge were pseudoreplicated. It is true that they all come from one prairie reconstruction and, compared to the isolated reconstructions, they cover less geographical space. The major problem with pseudoreplication that is relevant to this work would be a spatial autocorrelation among sites in a response variable (e.g., butterfly community composition) due to local soil type, management or habitat conditions. To minimize the influence of pseudoreplication on the results, sites on Neal Smith NWR were spaced as far apart as possible. Pseudoreplication was accepted because Neal Smith NWR was large and encompasses a fairly diverse landscape and because no other integrated reconstruction projects existed within the larger study area. The mean size of the planting units used as sites was 18.24 (range = 5–42) hectares. The landscape surrounding the refuge property is primarily agricultural.

The other 12 reconstructed sites and 12 prairie remnants were isolated areas of prairie in central Iowa (Fig. 1) hereafter referred to as "isolated reconstructions" and "remnants". Remnants averaged 11.53 (range = 6–25) hectares in size and the reconstructions had a mean of 17.29 (range = 6–33) hectares. We limited the size of prairies used in our study to avoid patch size effects. An ANOVA (Proc GLM; SAS Institute, 2000) indicated no significant differences in area among the three prairie types (remnant, isolated reconstruction and integrated reconstruction, $df = 2$, $F = 1.54$, $p = 0.229$) and there was no correlation between butterfly richness ($r = -0.14$, $p = 0.428$) or abundance ($r = -0.10$, $p = 0.552$) and site area. The surrounding landscape for these sites was always non-prairie and usually agricultural (58%, 14/24 sites) but sites could also be surrounded by forest (29%, 7/24 sites) or manicured lawn (13%, 3/24 sites).

All sites existed along a vegetative quality gradient ranging from a high to low level of plant diversity. A third of the remnant and isolated reconstructions and half of the integrated reconstruction sites were burned during the fall or spring preceding the surveys (14 burned, 22 unburned). A *t*-test between burned and unburned sites indicated that butterfly richness (but not abundance) was significantly different between the different management types ($df = 34$, $t = -2.13$, $p < 0.0402$), so the effect of burning was factored into our data analysis

Table 1
Least square (LS) means for all butterfly, habitat-sensitive (HS), and disturbance-tolerant (DT) species richness and abundance as well as plant diversity[1], and % native plant richness (% native)

Types of sites	*N*	Butterfly						Plant	
		Richness	Abundance	HS species richness	HS species abundance	DT species richness	DT species abundance	Diversity	% Native
Restored/Native[2]									
Remnant	12	9.13(0.79)a	13.48(2.66)a	1.50(0.30)a	1.92(0.39)a	4.88(0.37)a	9.94(2.68)a	10.03(1.06)a	0.80(0.02)a
Isolated	12	6.00(0.79)b**	11.73(2.66)a	0.50(0.30)b*	0.49(0.39)b**	4.38(0.37)a	11.31(2.68)a	6.63(1.06)b*	0.76(0.02)a
Integrated	12	8.00(0.75)ab	8.61(2.61)a	1.08(0.28)ab	0.67(0.36)b*	4.83(0.35)a	7.67(2.53)a	7.91(1.00)ab	0.67(0.02)b**
Quality level									
High	13	7.55(0.85)a	11.27(2.73)a	0.69(0.25)a	0.40(0.22)a	4.58(0.40)a	10.56(2.64)a	NA	NA
Low	11	6.17(1.04)a	8.48(3.32)a	0.69(0.31)a	0.67(0.27)a	4.46(0.48)a	6.96(3.21)a	NA	NA
Management[3]									
Burned	14	6.67(0.71)a	10.21(2.44)a	0.64(0.27)a	0.14(0.28)a	4.02(0.33)a	7.13(3.22)a	8.93(0.94)a	0.76(0.02)a
Unburned	22	8.75(0.56)b*	12.33(1.94)a	1.42(0.21)b*	0.87(0.23)b**	5.36(0.26)b**	10.28(2.65)a	7.46(0.74)a	0.72(0.02)a

LS mean estimates of butterfly and vegetation variables for restored/native and management result from a two factor ANOVA with factors type and management. LS means of butterfly richness and abundance for quality result from a two factor ANOVA with factors, quality and management. Numbers in parentheses following LS means are standard errors. Different lettered superscripts indicate significant differences.

[1] Plant diversity calculated using the Simpson index (Simpson, 1949).

[2] Isolated = isolated reconstructed prairie and integrated = Neal Smith NWR reconstructed prairie.

[3] Management designation based on whether a site was burned or not in the spring or fall prior to data collection.

* Significance at the $p > 0.05$ level.

** Significance at the $p > 0.01$ level.

(Table 1). Note that the sites were not chosen based on their management history; we were simply interested in accounting for the effect of a fire within the same year of surveys.

2.2. Data collection

Plants and butterflies were surveyed three times between May and August of 2003. Sites were surveyed in the same order in each round to maintain an evenly spaced time interval between visits. Butterfly and plant data for each site were collected within 0–2 days of each other. Butterflies were sampled using a transect method modified from Thomas (1983). Two 100×5 m transects were laid out at each site at least 100 m apart to minimize repeat sightings. The location of each transect was chosen to reflect the variability within a site and was marked for the duration of the study with pin flags. The researcher walked the transect at a steady pace of approximately 10 m/min for a total survey time of ten min. Every butterfly within a 5×5 m visual field in front of the observer was identified (usually by sight) and recorded. Sampling time did not include capture and processing of individuals or recording (i.e., stopwatches were stopped for these activities). Specimens that could not be identified in the field were captured, and taken into the lab for identification. Surveys were only conducted on warm (not below 18 °C), sunny (less than 60% cloud cover), and calm (sustained winds less than 17 km/h) days between 0930 and 1630 h. Data collected included the species name and the number of each species observed.

Vegetation sampling was conducted using 12 0.5×0.5 m quadrats at each site. One quadrat was installed every 20 m along each butterfly transect (six per transect). The data recorded included a description of the species present and a visual estimate of percent cover for each species as well as for litter and bare ground (modified from Daubenmire, 1959). Percent cover of each plant species was described as the proportion of the quadrat each species occupied in relation to all other live-plants. The % cover of litter and bare ground was the proportion each of these factors occupied in relation to each other and live-plant stem cover. The two observers standardized estimates of percent cover during the first round and plots were alternated between observers for the last two rounds in order to minimize observer bias. Number of ramets in bloom per species per quadrat was also noted to obtain an estimate of nectar availability.

The number of sampling replicates was established based upon analysis of species accumulation curve data. Plant species accumulation curves level out between seven and 10 replicates per site. Butterfly accumulation curves showed only slight increases in numbers of species added between two and three replicates per site.

2.3. Statistical analysis

2.3.1. Differences between remnant and reconstructed prairies

The butterfly communities in remnant and reconstructed prairies were compared based upon their

species richness, abundance, and composition. Species richness was defined as the total number of species observed at each site summed across the three rounds. Butterfly abundance was defined as the total number of individual butterflies observed summed across the two transects at each site and then averaged across three survey rounds. As a broad measurement of species composition, we used habitat affinities of butterflies described in the literature (Scott, 1986; Opler and Krizek, 1984; Ries et al., 2001) to select a subset of 14 butterfly species (the most frequently recorded in their respective categories), which were categorized as either habitat-sensitive (seven species) or disturbance-tolerant (seven species) (Table 2). Habitat-sensitive butterflies are those species found primarily in grasslands with relatively low anthropogenic disturbance; disturbance-tolerant species are common in many habitats regardless of disturbance level.

Vegetative quality of each site was assessed using measures such as plant diversity and the proportion of native plant species richness (% native). Plant diversity was determined by calculating Simpson's diversity index (Simpson, 1949) for each round using percent cover values and then averaging the indices across the three rounds to achieve one diversity value per site. Percent native refers to the proportion of total plant richness on each site composed of native species. These two primary variables (plant diversity and % native) were chosen as the most likely plant variables used by reconstruction practitioners to evaluate the development of the plant community. Other vegetation characteristics examined to quantify the relationship between the butterfly and

Table 2
A subset of 14 butterfly species (seven of the most frequently observed species in each category) was categorized into habitat-sensitive (HS species) or disturbance-tolerant (DT species)

	Native			Integrated			Isolated			Total		
	N	% of total	% Site occurrence	*N*	% of Total	% Site occurrence	*N*	% of Total	% Site occurrence	*N*	% of total	% Site occurrence
Disturbance-tolerant												
Everes comyntas Eastern-tailed blue	195	39%	91.7%	136	42%	100%	228	53%	100%	559	43%	97%
Colias eurytheme Orange sulphur	49	10%	91.7%	36	11%	83%	66	15%	75%	151	11%	83%
Colias philodice Clouded sulphur	56	11%	100%	43	13%	83%	44	10%	83%	143	11%	89%
Phyciodes tharos Pearl crescent	24	5%	75%	16	5%	58%	28	6%	75%	68	5%	69%
Danaus plexippus Monarch	17	3%	67%	31	10%	75%	16	4%	58%	64	5%	67%
Pieris rapae Cabbage white	13	3%	50%	7	2%	33%	5	1%	33%	25	2%	39%
Papilio polyxenes Black swallowtail	8	2%	42%	7	2%	50%	3	>1%	25%	18	1%	39%
Habitat-sensitive												
Cercyonis pegala Common wood nymph	43	9%	50%	1	<1%	8%	6	1%	17%	52	4%	25%
Speyeria idalia Regal fritillary	26	5%	50%	10	3%	42%	14	3%	25%	50	4%	39%
Lycaena dione Gray copper	3	1%	17%	5	2%	33%	7	2%	17%	15	1%	22%
Boloria bellona Meadow fritillary	12	2%	33%	0	0%	0%	0	0%	0%	12	1%	11%
Anatrytone logan Delaware skipper	1	<1%	8%	1	<1%	8%	0	0%	0%	2	<1%	6%
Chlosyne nycteis Silvery checkerspot	1	<1%	8%	1	<1%	8%	0	0%	0%	2	<1%	6%
Lycaena hyllus Bronze copper	0	0%	0%	1	<1%	8%	0	0%	0%	1	<1%	3%

HS butterflies were defined as those species found primarily in grasslands with relatively low anthropogenic disturbance while DT species were common in many habitats regardless of disturbance level. These designations were made by using habitat characterizations from the literature (Opler and Krizek, 1984; Scott, 1986; Ries et al., 2001). About 152 recorded individuals were not included in this analysis because they either did not fit in one of the categories (i.e., woodland species) or they were disturbance-tolerant species that did not occur in great enough numbers.

plant communities at each site included: the proportion of native plant cover relative to total vegetation cover (% native cover), the proportion of potential butterfly host plant cover relative to total plant cover (% host cover), the proportion of litter cover relative to bare ground (% litter cover), and the number of ramets in bloom (ramets) summed across all nectar-producing plant species.

A two-way analysis of variance (ANOVA) (Proc GLM; SAS Institute, 2000) was performed to detect differences in butterfly richness and abundance on sites of different type (native, isolated reconstruction, integrated reconstruction) and different management (burned or not burned during the spring or fall preceding the survey season). This ANOVA was repeated for the two main vegetative variables (plant diversity, % native) and for richness and abundance of HS and DT butterflies. Contrast statements were used to compare differences between treatments.

2.3.2. Recovery of reconstructed prairies

Four analyses were used to determine how the butterfly community responded to the state of the plant community on reconstructed prairies. Correlations were performed between butterfly richness and abundance and the two vegetative measures: plant diversity and % native. Vegetative rankings of the reconstructed prairies were determined by first calculating the average value of each variable (plant diversity and % native) for all remnant (reference) sites. These mean values from the reference prairies were established as the "goal" value for each reconstructed site. Plant diversity and % native values for each reconstruction site were then divided by the goal value and these values were averaged to achieve one %-recovered value for each reconstruction (Appendix A). Sites with a % recovered value of 80% or less were labeled low quality ($N = 11$), and sites with %-recovered values higher than 80% were labeled high quality ($N = 13$). The 80% recovered figure represents the value approximately halfway between the observed range of 47–117% recovered value. Differences between recoveries were assessed using a two-way ANOVA with burning status as a grouping variable.

To examine whether the butterfly and plant communities exhibit similar trends on reconstructed prairies, %-recovered values were also calculated using butterfly richness and abundance and these values were used to perform a Spearman's rank correlation with the vegetative %-recovered values. For butterflies, only nine sites fell into the high quality category. Butterfly species compositions were tested for differences between different reconstruction quality levels and remnant prairies. A two factor ANOVA on prairie quality and management was performed to determine whether higher quality prairies supported higher levels of habitat-sensitive butterfly species.

2.3.3. Vegetative predictors of butterfly occurrence

The final analysis used was an all-subsets ($C(p)$) multivariate regression analysis (PROC REG; SAS Institute, 2000) to determine which vegetation characters were the most highly correlated with butterfly richness and abundance. All plant variables listed in Section 2.3.1 were examined for strong correlations ($r > 0.55$) and for those that were strongly correlated, one variable was dropped from the final regression analysis to avoid collinearity. The final list of independent variables used was: ramets, % litter, % native cover, area, and % host cover. The standardized slope values of the variables in the best model were examined to determine whether the predictive direction was negative or positive.

3. Results

One hundred and eighty plant species and 37 butterfly species were identified over all sites during 2003. Butterfly individuals recorded totaled 1314, which included 134 of the seven HS species and 1028 of the seven DT species (Table 2). The prairie remnants supported 29–65 plant species and 6–11 butterfly species. Across all reconstructions plant species richness varied from 14 to 48 and butterfly species richness ranged between 2 and 14. *Cercyonis pegala* and *S. idalia* were the most numerous butterfly species in the habitat-sensitive group, while *Everes comyntas* and two *Colias* species were the most numerous species in the disturbance-tolerant group. Because *E. comyntas* accounted for 43% of the butterfly abundance total, we tested its effect on the overall community analysis results. Removing it from analyses made no significant difference in the results.

3.1. Differences between remnant and reconstructed prairies

Plant diversity was significantly higher on remnant prairies than on isolated reconstructions (Table 1). Percent native plant richness was significantly higher on remnants and isolated reconstructions than on integrated reconstructions (Table 1). Comparing burned and unburned sites, there were no significant differences in either plant diversity or percent native plant richness.

Butterfly richness was significantly higher on remnant prairies than on isolated reconstructions (Table 1). Butterfly abundance showed no significant differences among prairie types though it was highest on remnants. Habitat-sensitive butterfly richness was significantly higher on remnant prairies versus isolated reconstructions and habitat-sensitive abundance was significantly higher on remnants compared to both integrated and isolated reconstructions. Disturbance-tolerant butterflies

exhibited no significant difference in richness or abundance among different types of prairies (Table 1).

3.2. Recovery of reconstructed prairies

Both total butterfly richness and abundance were highest on high quality reconstructions (Table 1). In addition, disturbance-tolerant butterfly abundance was also highest on higher quality reconstructions. However, the difference between high and low quality reconstructions for all butterfly richness and abundance measures was not significant.

Both total butterfly richness and abundance were highest on unburned prairies, but the trend was only significant for butterfly richness (Table 1). Habitat-sensitive species showed significantly higher richness and abundance on unburned prairies; disturbance-tolerant butterfly richness was also higher on unburned prairies.

There were no significant Spearman's rank correlations between %-recovered values using vegetation versus butterflies, which suggested that there was no correlation in how butterfly and plant community measures ranked reconstructed prairies ($r = -0.046$, $p = 0.831$).

3.3. Vegetative predictors of butterfly occurrence

The best predictors of butterfly richness on a site were the amount of nectar (# ramets) and the % cover of litter. Analysis of the standardized slope indicates a positive relationship between butterfly richness and number of ramets and % litter. The regression model including ramets, and % litter explained 31% of the variation (Table 3). Note that the correlation between ramets and % litter was not significant ($r = -0.273$, $p > 0.11$) so it was deemed acceptable to include both variables in the regression. We did not include both ramets and % forbs because % forbs was correlated with % litter. Butterfly abundance was not highly correlated with any of the vegetative components used in producing the regression model (Table 3). There were also no significant correlations between butterfly richness and abundance and plant diversity or % native plants within the reconstructed and remnant prairies.

Table 3
Vegetation variables that were best predictors of butterfly richness and abundance on all prairie sites

Butterfly variables	N	$C(p)$	R^2	Variables in best model	Standardized B (slope)
All sites					
Richness	36	2.00	0.31*	Ramets	0.481
				% Litter	0.436
Abundance	36	0.76	0.13	Ramets	0.274
				% Litter	0.324

Models were calculated using an all-subsets multivariate regression with the following variables: % native plant species cover, % native plant species richness, number of ramets in bloom, % cover of litter, % host plant cover and area.

* R^2 is significantly different from zero at $p > 0.01$ level.

4. Discussion

4.1. The importance of remnant prairie habitat

As expected, remnant prairies supported higher numbers of butterfly species and higher values for the primary plant variables (diversity and % native) than reconstructed prairies. This trend has been found for a number of organisms in other grassland studies (Panzer et al., 1995; Wheater and Cullen, 1997; Brand and Dunn, 1998; Bomar, 2001) but is not universal (Bisevac and Majer, 1999). Integrated reconstructions did not differ significantly in butterfly richness from remnant prairies, placing them in an intermediate position between prairie remnants and isolated reconstructions. Integrated reconstructions supported higher plant diversity than isolated reconstructions, but ranked lowest in % native plant species, so average vegetation quality was not superior to isolated reconstructions. While many other factors may be involved in influencing higher butterfly richness at Neal Smith NWR (our example of integrated reconstructions), a plausible explanation is the clustered nature of the restorations, the landscape-scale of the project, and the integration of small patches of remnant vegetation, thus providing adjacent sources for colonization and a larger area of suitable habitat. We attempted to limit spillover by placing our integrated planting units 310 m or more from a remnant prairie. However, this distance may have been too small to limit movement entirely. This provides some clues that butterflies probably are moving on the order of 300 m between reconstruction patches within an integrated restoration. Thus, placing restorations 300 m apart may be advantageous in other restoration projects involving butterflies. Fry and Main (1993) advocate the consideration of landscape context and the potential for colonization and movement in reconstructing fragmented ecosystems. Steffan-Dewenter and Tscharntke (2002) found that butterfly species richness overall and the proportion of monophagous species was higher on larger grassland fragments. In montane wetlands, Wettstein and Schmid (1999) reported that butterfly richness, especially of wetland specialists, was positively related to habitat area and the amount of suitable habitat in a 4-km radius of the study site.

Remnant prairies supported significantly greater richness and abundance of habitat-sensitive butterfly species and integrated reconstructions were again in the intermediate position (between remnants and isolated

reconstructions) for habitat-sensitive species abundance, further supporting Wettstein and Schmid (1999) and Steffan-Dewenter and Tscharntke (2002). Panzer et al. (1995) designated remnant-dependent arthropods based on the degree of their reliance on remnant prairies. Our habitat-sensitive species might be viewed as similar to Panzer's remnant-dependent species. Because our studies were conducted in different regions of the Midwest, the suite of species is not the same, but they fill a similar niche. The fact that disturbance-tolerant species exhibited no difference in richness or abundance among prairie types highlights their generalist approach to habitat use. Kitahara and Fujii (1994) examined specialist vs. generalist butterfly species richness along an anthropogenic disturbance gradient and found that specialists differed among treatments while the number of generalist species did not. The preference of habitat-sensitive butterfly species for remnant prairie suggests that these prairies are refuges (and potential sources) for many habitat-sensitive butterfly species. The trend towards higher numbers of habitat-sensitive butterflies on integrated reconstructions when compared to isolated reconstructions demonstrates the utility of integrating reconstructions with remnants to encourage these butterfly species.

4.2. Assessment of vegetative quality on reconstructed prairies

Abundance and richness of butterflies was higher on reconstructed prairies with high vegetative quality, but this trend was not significant. Related research in Iowa on both prairie and other types of grasslands has shown that butterfly abundance increases with greater floral resources (Skibbe and Debinski, unpublished data). Several recent studies examining a single butterfly species have found that habitat quality is an important factor in determining population dynamics (abundance) and behavior (i.e., number and location of eggs) (Dennis and Eales, 1999; Kopper et al., 2000; Fleishman et al., 2002; Fownes and Roland, 2002; Matter and Roland, 2002). However, it may be more difficult to pinpoint trends related to habitat quality when examining the full butterfly community, which contains many species exhibiting different habitat requirements or tolerances (Pywell et al., 2004). Other studies have shown butterflies to be poorly linked to vegetative diversity (Kremen, 1992; Holl, 1996). In fact, butterfly richness may respond positively to increased exotic plant cover (Simonson et al., 2001), which is often inversely correlated with diversity and would be negatively associated with vegetative quality in this study. Finally, some of our remnant prairies were heavily degraded by infiltration of invasive grasses and woody plants and supported a truncated butterfly species assemblage (excluding many of the prairie specialists). As the butterfly community in remnants becomes more generalized, one would expect that it would become more difficult to find statistically significant differences between remnants and reconstructions.

The strong response of butterfly richness and abundance to a prairie's burn status, % cover of litter, and # ramets reflects the importance of management in providing good butterfly habitat. Burning has both positive and negative effects on the butterfly community. It can enhance the flowering of a prairie, but it may also kill Lepidopteran eggs or larvae. If the frequency of burning is too low, the nectar resources (# ramets) may decrease. This study and several others (Holl, 1995; Loertscher et al., 1995; Matter and Roland, 2002; Pywell et al., 2004) have found that nectar resources are of primary importance in determining butterfly occurrence. However, during periods immediately after a burn (as evidenced by reduced % cover of litter), the butterfly species richness is lower.

5. Conclusions

As expected, reconstructed prairies never ranked as highly in butterfly species richness or abundance as compared to restored prairies. The differences in species richness and abundance on remnant versus reconstructed prairies indicate that most prairie reconstructions in central Iowa have not reached the level of butterfly community diversity present on remnants. However, the most interesting result from this research is that clustered reconstructions showed intermediate responses in overall butterfly richness and habitat-sensitive species richness between those of prairie remnants and isolated reconstructions. These results provide important documentation of the value of integrated reconstructions in the conservation of habitat restricted butterfly species.

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Appendix A

Percent recovered (%-recovered) values for vegetation and butterflies on all reconstructed prairies

Reconstructed sites	Plants				Butterflies			
	Diversity	% Native	Mean % -recovered	Quality level	Richness	Abundance	Mean % -recovered	Quality level
Reference mean	**9.88**	**0.795**			**9.17**	**13.83**		
NSNWR1	14%	79%	**47%**	Low	98%	46%	**72%**	Low
Colo Bogs	33%	80%	**56%**	Low	55%	53%	**54%**	Low
NSNWR70	43%	70%	**57%**	Low	98%	154%	**126%**	High
Jester Park	26%	89%	**57%**	Low	98%	111%	**105%**	High
NSNWR26	35%	84%	**59%**	Low	22%	46%	**34%**	Low
NSNWR25	43%	76%	**60%**	Low	109%	70%	**90%**	High
Big Creek	34%	99%	**67%**	Low	76%	39%	**58%**	Low
NSNWR17	65%	79%	**72%**	Low	66%	31%	**48%**	Low
McFarland	50%	96%	**73%**	Low	44%	10%	**27%**	Low
Meetz	54%	93%	**73%**	Low	55%	65%	**60%**	Low
Prairie Flower	48%	101%	**74%**	Low	120%	121%	**120%**	High
Richard's Marsh	62%	98%	**80%**	High	44%	19%	**32%**	Low
NSNWR23	76%	90%	**83%**	High	66%	19%	**42%**	Low
Briggs Woods	64%	104%	**84%**	High	33%	15%	**24%**	Low
Grimes Farm	78%	98%	**88%**	High	22%	41%	**31%**	Low
NSNWR10	100%	79%	**89%**	High	87%	55%	**71%**	Low
NSNWR21	103%	85%	**94%**	High	142%	87%	**114%**	High
NSNWR42	91%	100%	**95%**	High	76%	27%	**52%**	Low
Stargrass	92%	104%	**98%**	High	44%	99%	**71%**	Low
NSNWR19	109%	98%	**103%**	High	120%	101%	**101%**	High
Hanging Rock	127%	86%	**107%**	High	153%	157%	**155%**	High
Prairie Creek	113%	100%	**107%**	High	87%	321%	**204%**	High
NSNWR44	131%	95%	**113%**	High	98%	84%	**91%**	High
NSNWR31	151%	84%	**117%**	High	66%	27%	**40%**	Low

Vegetative rankings of the reconstructed prairies were determined by first calculating the average value of each variable (plant diversity, % native, etc.) for all remnant (reference) sites (in table, reference mean). These mean values from the reference prairies were established as the "goal" value for each reconstructed site. Plant diversity, and % native values for each reconstruction site were divided by the goal value for each variable and then averaged to obtain a %-recovered value. Sites with %-recovered values higher than 80% were labeled high quality, and sites with % recovered values 80% or less were labeled low quality. Butterfly %-recovered values and rankings of prairies were determined in the same manner as the vegetation but using butterfly richness and abundance values.

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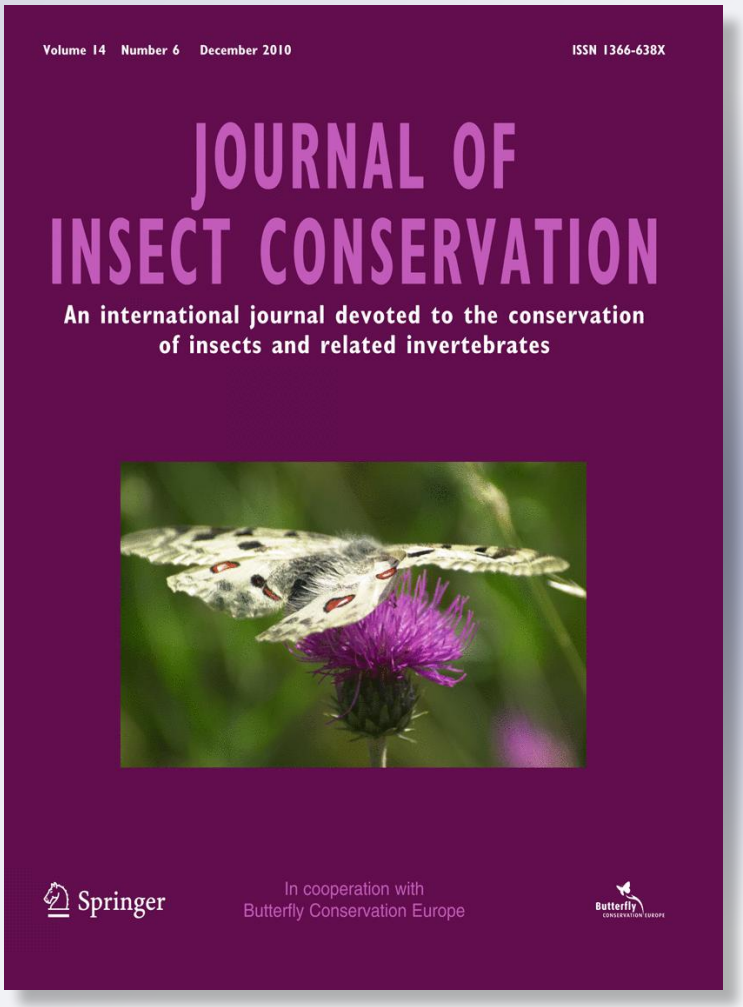

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Direct and indirect responses of tallgrass prairie butterflies to prescribed burning

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Abstract Fire is an important tool in the conservation and restoration of tallgrass prairie ecosystems. We investigated how both the vegetation composition and butterfly community of tallgrass prairie remnants changed in relation to the elapsed time (in months) since prescribed fire. Butterfly richness and butterfly abundance were positively correlated with the time since burn. Habitat-specialist butterfly richness recovery time was greater than 70 months post-fire and habitat-specialist butterfly abundance recovery time was approximately 50 months post-fire. Thus, recovery times for butterfly populations after prescribed fires in our study were potentially longer than those previously reported. We used Path Analysis to evaluate the relative contributions of the direct effect of time since fire and the indirect effects of time since fire through changes in vegetation composition on butterfly abundance. Path models highlighted the importance of the indirect effects of fire on habitat features, such as increases in the cover of bare ground. Because fire return intervals on managed prairie remnants are often less than 5 years, information on recovery times for habitat-specialist insect species are of great importance.

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Introduction

Grassland ecosystems across the globe have been degraded by the disruption of their natural disturbance regimes. Fire is an important component in the disturbance regimes of many ecosystems (Sauer 1950; Vieira et al. 1996; Fleishman 2000; Huntzinger 2003) and it is particularly important in grassland ecosystems (Collins and Gibson 1990; Schultz and Crone 1998). After a period of fire suppression in the management of grassland ecosystems, it has become apparent in many places that fire plays an important positive role in their maintenance (Collins and Gibson 1990).

The tallgrass prairie region of North America is one of the most endangered ecosystems on Earth (Smith 1981; Noss et al. 1995) and it is dependent on fire for its persistence. In fact, Axelrod (1985) recognized that, after climate, fire is the most significant factor that influences the composition of tallgrass communities. The land area of Iowa was once 85% tallgrass prairie (Smith 1981) yet today less than 0.01% of the over 12 million original hectares of prairie remain (Sampson and Knopf 1994). Tallgrass prairie remnants in Iowa are small and isolated components of the modern landscape. The fragmented and isolated nature of modern grasslands do not allow for the mosaic of burned and unburned areas historically associated with grassland fire cycles. The Loess Hills of western Iowa contain some of the state's largest unplowed native grasslands (Mutel 1989). This unique landform is composed of a band of steep ridges and narrow valleys along the eastern side of the Missouri River (Orwig 1990). Prior

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to European settlement of the Loess Hills area, mean fire frequency was estimated to be 6.6 years based on analysis of tree ring and fire scar data (Stambaugh et al. 2006). Following settlement, intentional fire suppression in the Loess Hills led to the encroachment of shrubs and trees into remaining grasslands (Mutel 1989). Current management strategies for the Loess Hills include more frequent prescribed fires conducted every 1–5 years.

Fire effects on grassland vegetation

Fire has extensive effects on the native vegetation of the North American Tallgrass Prairie Region, including effects on the development, productivity, and reproduction of native plants. Burning tallgrass prairie removes both the litter layer and standing dead plant material, exposing the soil surface to the sun. This exposed soil surface area results in higher soil temperatures early in the growing season and leads to earlier development of vegetation (Hulbert 1984; Pauly 1997). The seed production and flowering of warm-season grasses is increased by spring burning (Hulbert 1984, 1988; Glenn-Lewin et al. 1990). Cool-season grasses tend to respond in the opposite way; their flowering and reproduction are lessened by spring burning (Hulbert 1984, 1988). Because many of the cool-season grasses including Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) found on prairie remnants are non-native invaders, their reduced flowering and reproduction may be a beneficial result of prescribed burning (DiTomaso et al. 2006). Although fire has been a significant evolutionary force in the development of the tallgrass prairie ecosystem, the severe fragmentation and subsequent isolation of the remaining small patches has affected their ability to function in response fire.

Fire effects on invertebrates

Studies of butterflies and insects from different regions of the globe have indicated that species have different habitat requirements at each life stage. Thus, populations at each life stage can respond differently to disturbance (New et al. 1995; Samways 2007). Fire has increasingly been used as a management tool for restoring native habitats (Hobbs and Atkins 1990; Panzer and Schwartz 2000; Huntzinger 2003). Some researchers have expressed concern about the response of insect species to prescribed fire in small, isolated remnants (Dana 1991; Swengel 1996; Panzer 2002; Samways 2007). Although the extent of insect mortality as a direct result of a fire is unknown, it is potentially substantial. Local populations of insects on fragmented preserves may not survive repeated prescribed burns (Panzer 2002).

Because fire is a historical part of the tallgrass prairie ecosystem, it may be reasonable to assume that the invertebrate inhabitants of this region have evolved mechanisms that allow them to survive during frequent fire events (Panzer and Schwartz 2000). However, considering that most of the land in the tallgrass prairie region has been converted for human use and the remaining native prairie exists in highly fragmented patches, ecosystem function may have been compromised.

The invertebrate communities of tallgrass prairies comprise a large proportion of the total biodiversity in the ecosystem and their survival is an important issue for conservation (Dietrich 1998). Past researchers have shown that fire can have significant negative effects on the species richness and abundance of prairie invertebrates. Certain habitat-specialist butterfly species, including several species of skippers (*Oarisma powesheik*, *Hesperia ottoe*, *H. dacotae*, *H. leonardus*, *Atrytone arogos*) and the regal fritillary (*Speyeria idalia*) have been shown to suffer negative effects from fire with effects continuing for approximately 5 years post-fire (Swengel 1996). The relative mobility and dispersal ability of insects during the adult stage may be a significant factor in mitigating the negative effects of fire for fire-sensitive and specialist species (Swengel 1996).

Although the short-term responses of insects to fire can be either positive or negative, remnant dependent and non-vagile species are most likely to be negatively affected immediately after a fire (Panzer 2002). Knowledge of insect population recovery times could prove important to land managers when decisions are made about how long to wait between prescribed burns.

Our objective was to determine how both the butterfly community and vegetation composition of tallgrass prairie remnants changed at a site in response to prescribed fire by answering the following questions:

1. How do butterfly abundance, butterfly species richness, and vegetation composition of tallgrass prairie remnants change in relation to the elapsed time since the site was burned?
2. What are the relative contributions of direct and indirect effects of time since fire on butterfly abundance and butterfly species richness?

Study area

We conducted our study on prairie remnants located in Plymouth County, Iowa, USA at the northern end of the Loess Hills Landform (Fig. 1). Specifically, survey sites were located on Broken Kettle Grasslands Preserve (more than 1,800 ha owned and managed by The Nature Conservancy, located in T91N, R48W, Sections 6, 7, 8, 18, 19 and T91N, R49W, Sections 1, 12, 13, 14), Five Ridge Prairie (approximately 320 ha, owned and managed by the

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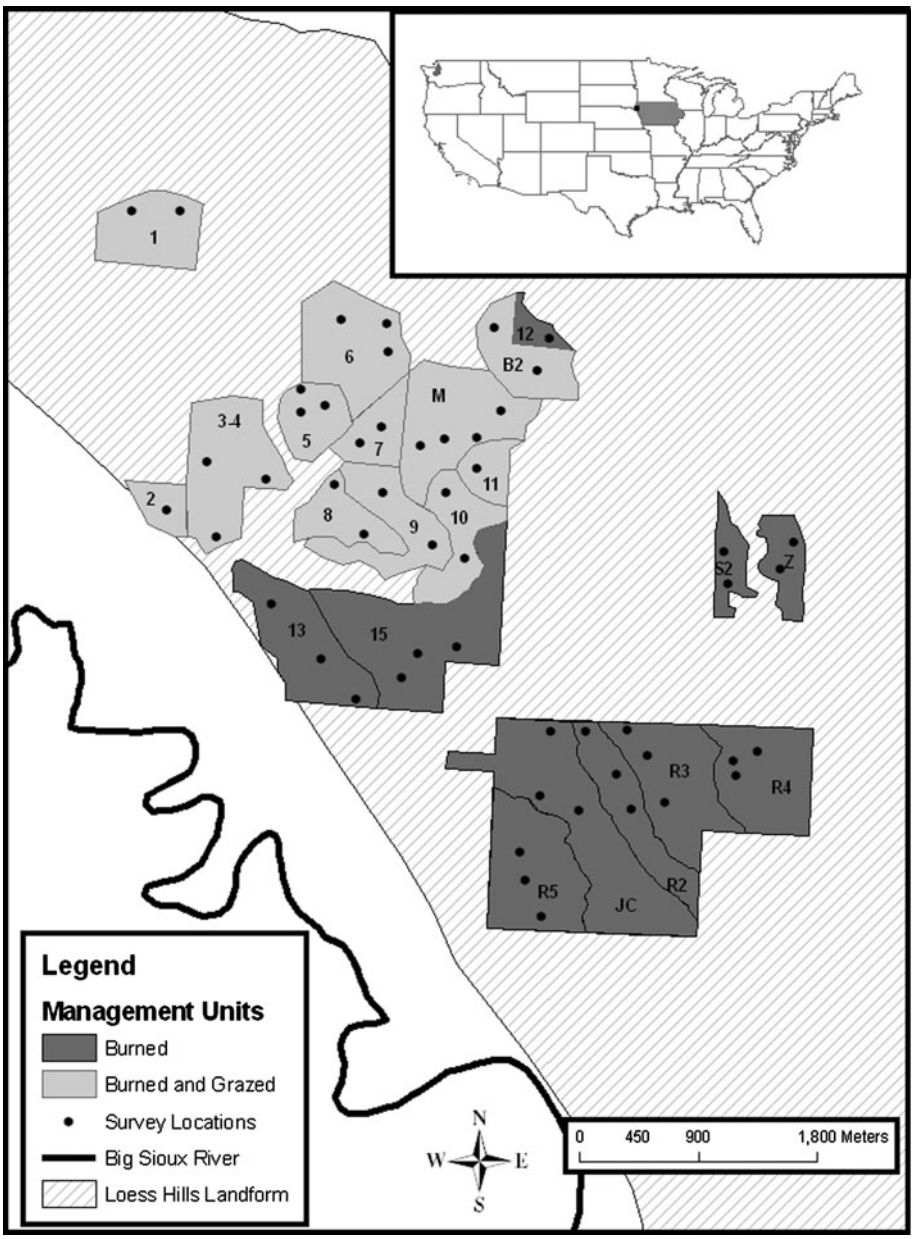

Fig. 1 Map of study sites with management unit boundaries and butterfly survey plots surveyed during 2004 and 2005. All sites were located in Plymouth County, Iowa, USA. Study sites included Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land. See "Appendix B" for information about fire management history on each management unit

Plymouth County Conservation Board, located in T91N, R48W, Sections 20, 21, 28, 29), and on adjacent private land.

Methods

We surveyed 53 plots within 22 management units between 1 June 2004 and 15 August 2005. Management units ranged in size from approximately 10–70 ha, with an average size of 40 ha. The study area was managed with prescribed fires conducted during the fall and spring in 2–6 year rotations (S. Moats, Director of Stewardship, Iowa Chapter of The Nature Conservancy, personal communication). Twelve of the management units (27 survey plots) were also managed with light grazing by domestic cattle with stocking rates of approximately 0.25 cow–calf pairs/ha. Grazing in this system was used as an ecological management tool and grazing intensity was much lighter than in a system where grazing is primarily for economic gain. Present management regimes were in place in all units for a minimum of 4 years. Within each management unit, we located survey plots using a stratified sampling design. We placed survey plots randomly with the restrictions that they were at least 150 m apart and at least 50 m from any unit edge or woody edge. Depending on the size of each management unit, we established 1–3 survey plots in each of the management units. Using the above sampling design,

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there were 26 survey plots in 10 burned only management units, and 27 survey plots in 12 burned and grazed management units (Fig. 1, "Appendix B").

Vegetation surveys

We measured the vegetation at each survey plot twice each year in June and July of 2004 and 2005 to coincide with the peak biomass of cool- and warm-season grasses. Vegetation variables we measured included litter depth, percent cover of warm-season grasses, percent cover of cool-season grasses, percent cover of native forbs, percent cover of exotic forbs, and percent cover of bare ground. We chose vegetation components to measure based on their expected influences on butterfly abundance. We measured the percent cover variables by placing a 0.5 × 0.5 m Daubenmire frame (Daubenmire 1959) on the ground at locations 5 and 25 m away from the center of the plot in each cardinal direction. We determined the percent cover of each vegetation type visually within the sampling frame rounded to the nearest 5%. We measured litter depth in millimeters using a ruler at center of the sampling frame. For all of the vegetation variables, we averaged the measurements taken at each of the eight locations within a plot for each management unit.

Floral resource surveys

Immediately following each butterfly survey, we conducted a floral resource survey on each of the 50 × 50 m plots to assess the availability of floral resources on the plot. One observer walked a 0.5 m wide transect diagonally across the plot counting the number of flowering ramets of forb species within the transect. We included only forb species known to be visited by adult butterflies for nectar resources in our dataset.

Butterfly surveys

We conducted two rounds of butterfly surveys each year in June, July, and August of 2004 and 2005. Round one lasted from early June through early July; round two lasted from early July to early August. We surveyed butterflies in 50 × 50 m plots at each survey plot on warm (21–35°C), sunny (less than 50% cloud cover), and calm (winds less than 16 km/h) days between 1,000 and 1,730 h. By restricting butterfly surveys to days that met the above weather and daytime requirements, we minimized the influence of weather conditions on the results of our surveys. During a survey, two observers walked systematically through the plot in a zigzag pattern and netted individuals observed for 30 min. We built this approach upon previous construction of sampling effort curves that showed 30 min to be an adequate time for sampling (e.g., Debinski and Brussard 1994). Butterflies that we observed but did not net were recorded as such, with careful attention so that they were not recorded twice. We placed netted butterflies in glassine envelopes with the time of capture recorded for each. At the end of the survey, we recorded data for each individual, including the species name, activity at the time of capture, and sex (if known). We released all butterflies at the completion of the survey unless their identity could not be confirmed. We collected unidentified individuals as voucher specimens and identified them in the lab. Two individuals (skippers) that could not be identified were excluded from the dataset. In analyses, we refer to the number of individuals observed as abundance. Analyses of abundance were conducted on individual species, all species (total butterfly abundance), and ecologically defined groups of species.

Data analysis

We categorized butterflies a priori into three mutually exclusive groups (habitat-specialist, habitat-generalist, and woodland species) based on their requirements for host plants and floral resources (Ries et al. 2001; Reeder et al. 2005; Shepherd and Debinski 2005; Davis et al. 2007; Vogel et al. 2007; see "Appendix A"). We considered a species to be a habitat-specialist if it relies on native prairie plant species for either its larval food or adult nectar resources. In Iowa, habitat-specialist butterflies are found primarily in native prairie habitat. However, habitat-specialist species may also be found in open woodland/savanna habitats with native grass/forb understory in some areas. Habitat-generalists use a variety of common plant species (both non-prairie natives and non-natives) and are common in a wide variety of open areas including yards, roadsides, and agricultural areas. Butterfly species that we categorized as woodland species utilize woodland plants for their host and floral resources. In contrast to the habitat-specialist group, woodland species are found primarily in closed canopy woodlands and woodland edges in Iowa. Our habitat-generalist group corresponds to the "disturbance-tolerant" category of Ries et al. (2001), Reeder et al. (2005), Shepherd and Debinski (2005), Davis et al. (2007), and Vogel et al. (2007). Previous uses of the term "disturbance-tolerant" referred to disturbances such as removal of vegetation. We changed the terminology here to prevent misinterpretation of the word "disturbance". Only species in the habitat-specialist and habitat-generalist groups were included in our analyses.

For each round of vegetation, floral resource, and butterfly surveys for each year, we determined the time (in months) since a fire had occurred from manager and land owner records. Each survey round for each of the 53 survey plots was assigned the number of months since a fire at the time of the survey. We examined the relationships of

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vegetation and butterfly variables to time since burn using repeated measures regression using PROC MIXED in SAS Version 8.2 (SAS Institute, Cary, NC, USA). Because each survey location within a management unit was not independent, we accounted for the nested structure of our sampling design (survey plots nested within management units) and for the repeated surveys on each plot (two rounds each year for 2 years) in the models. For each butterfly response variable, we examined regression models that included both a linear term and a quadratic term. When the quadratic term in the model was significant ($P < 0.05$), indicating that a linear term alone was not sufficient to explain the relationship, we presented models that included both the linear and quadratic terms (Sokal and Rohlf 1969). We analyzed individual butterfly species responses only if they had abundance of greater than 20 individuals summed across both years and were present on at least 40% of the survey plots (see "Appendix A" for species that met these criteria). To determine whether the season of the last burn conducted (fall or spring) or the size of the burn area had an effect on total butterfly abundance, we first ran regression models that included season of last burn and burn area. Neither season of last burn nor burn area were significant predictors of butterfly abundance in these models, so we did not include them in our subsequent analyses. Although some sites were managed with rotational grazing in addition to fire, we did not include grazing in our analyses (see Vogel et al. 2007 for a detailed examination of the treatment effects of fire vs. grazing). Rather, the present study examines the effects of fire and responses to specific components (described here as "indirect effects") of the vegetation such as litter, bare ground, and warm season grass cover with respect to butterfly recovery times. We are implicitly assuming that any effect of grazing will operate through its effects on vegetation.

To model the relative contributions of direct and indirect effects in the correlations between fire (measured as time since burn) and butterfly abundance, we used multiple linear regression in Mplus Version 5 (Muthen and Muthen, Los Angeles, CA, USA) and Path Analysis. Path Analysis is a statistical method originally proposed by Wright (1934) as a way to measure the direct and indirect relationships of color pattern inheritance in small mammals. Although the method has not been widely used by biologists (Shipley 2000), it is a technique that can effectively test an a priori hypothesis about causal relationships among variables (Wootton 1994). Essentially, Path Analysis is performed by conducting a series of correlations and multiple regressions to test a pre-defined hypothesis about the relationships between variables of interest (Wootton 1994). The result is a method by which the correlation between variables can be decomposed and the relative strengths of indirect and direct effects can be estimated (Wootton 1994).

We constructed Path Diagrams (Fig. 2) and conducted Path Analysis for butterfly abundance variables including total abundance and richness, habitat-specialist abundance and richness, and the abundance of seven individual species (*Cercyonis pegala*, *Colias eurytheme*, *Euptoieta claudia*, *Hesperia ottoe*, *Pieris rapae*, *Speyeria cybele*, and *S. idalia*) that had significant relationships with time since burn. The direct effect we examined was time since burn. The vegetation characteristics (indirect effects) that we examined were floral resource availability, percent cover of warm-season grasses, and percent cover of bare ground. We accounted for the nested structure of our sampling design and for the repeated surveys on each plot. We ran multiple regressions using the correlation matrix and standardized beta estimates. We calculated indirect effects by multiplying the correlation (from correlation matrix, Table 1) by the standardized path coefficient (Table 2) for each of the three

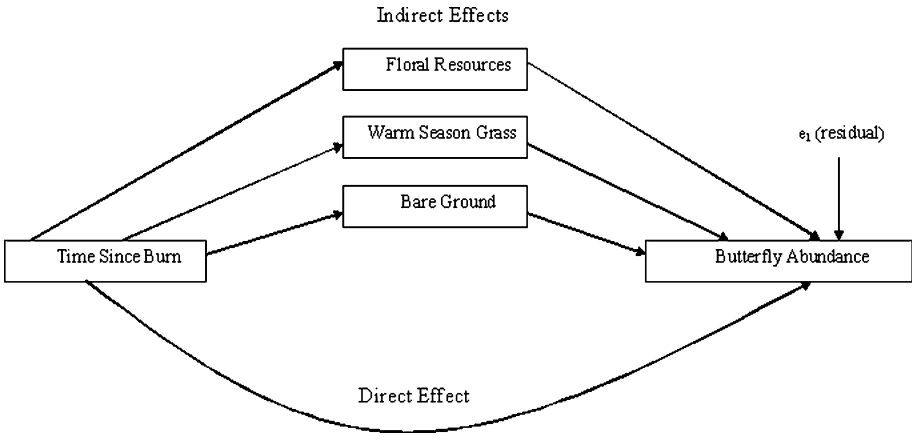

Fig. 2 Path diagram of proposed direct and indirect relationships between time since burn, vegetation characteristics, and butterfly abundance. All path models in the present study were based on this diagram using separate multiple regressions for each butterfly abundance variable. Independent variables chosen for inclusion in the path models were: Floral Resources (number of flowering ramets), Warm-season Grass (percent cover of warm-season grasses), and Bare Ground (percent cover of bare ground)

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Table 1 Correlations of variables used in path analysis including time since burn (TSB) in months, number of flowering ramets (Floral), percent cover of warm-season grasses (WS), percent cover of bare ground (BG), total butterfly richness (TR), habitat-specialist butterfly richness (HSR), total butterfly abundance (TA), habitat-specialist butterfly abundance (HSA), *Cercyonis pegala* (*C. peg*) abundance, *Colias eurytheme* (*C. eur*) abundance, *Euptoieta claudia* (*E. cla*), *Hesperia ottoe* (*H. ott*) abundance, *Pieris rapae* (*P. rap*) abundance, *Speyeria cybele* (*S. cyb*), and *Speyeria idalia* (*S. ida*) abundance

	TSB	Floral	WS	BG	TR	HSR	TA	HSA	*C. peg*	*C. eur*	*E. cla*	*H. ott*	*P. rap*	*S. cyb*	*S. ida*
TSB	1.00	−0.04	−0.19	−0.62	0.17	0.20	0.35	0.35	0.26	0.32	−0.14	−0.09	0.30	−0.22	0.24
Floral	−0.04	1.00	0.03	−0.04	0.12	0.12	0.14	0.05	0.05	0.16	0.30	0.12	0.06	0.09	0.14
WS	−0.19	0.03	1.00	0.10	0.19	0.09	0.03	0.03	0.03	−0.21	0.14	0.19	0.05	0.03	0.05
BG	−0.62	−0.04	0.11	1.00	−0.14	−0.28	−0.40	−0.43	−0.36	−0.27	0.21	0.02	−0.14	0.16	−0.30

paths tested. We summed the three indirect paths to obtain overall indirect effects for each model (see Fig. 2).

Results

Six vegetation characteristics that we measured were correlated with time since burn (Fig. 3). Not surprisingly, litter depth increased and the percent cover of bare ground decreased with time since burn. For bare ground, the highest percent cover occurred in the first growing season following the fire (<12 months). After the first growing season, the percent cover of bare ground decreased dramatically and then leveled off (Fig. 3). Floral resource availability decreased with time since burn. The percent cover of warm-season grasses increased slightly immediately post-burn, but appeared to quickly level off and decline slightly as time since burn increased (Fig. 3). Forb cover had only a marginal relationship with time since burn. Native forb cover had a weak negative association with time since burn and exotic forb cover had a weak positive relationship with time since burn (Fig. 3). Only the percent cover of cool-season grasses was not correlated with time since burn.

We observed 2,779 individual butterflies of 49 species during the study period. Of those, 1,385 individuals represented 18 habitat-specialist species and 1,305 individuals represented 26 habitat-generalist species ("Appendix A"). The most common species in the study area were *Cercyonis pegala*, *Speyeria idalia*, and *Colias eurytheme* ("Appendix A"). Three species encountered in the study area (*S. idalia*, *Hesperia ottoe*, and *Atrytonopsis hianna*) were species of conservation concern in Iowa (IDNR 2006).

Total butterfly richness and habitat-specialist butterfly richness were positively correlated with time since burn (Fig. 4). Total butterfly abundance and habitat-specialist butterfly abundance were also positively correlated with time since burn (Fig. 4). Of the 14 individual butterfly species we tested, seven species' abundances were correlated with time since burn (Figs. 5, 6).

We considered the recovery time of butterfly richness and abundance to be the point at which the relationship of richness or abundance with time since burn leveled off, although we could not know how complete the recovery was because we did not have data on pre-burn richness or abundance. Butterfly richness (total and habitat-specialist) and total butterfly abundance did not level off or decline with time since burn. For habitat-specialist butterflies as a group, abundance increased with time since burn up to approximately 50 months post-fire, then started to decline. For the four individual habitat-specialist species that had a relationship with time since burn, one species, *H. ottoe*, reached a point of decline in abundance at about 30 months, and one, *C. pegala*, reached an asymptote in abundance at about 50 months (Fig. 5). One habitat-specialist species, *S. cybele*, had a negative relationship with time since burn, and one species, *S. idalia*, had a positive relationship that did not level off even after 70 months post-fire (Fig. 5). Two of the habitat-generalist species, *C. eurytheme* and *P. rapae*, had positive relationships with time since burn and one habitat-generalist species, *E. claudia*, had a negative relationship with time since burn (Fig. 6).

The effects of prescribed fire could affect butterflies directly (direct mortality) or indirectly by creating changes in the vegetation composition and structure. For total butterfly abundance and richness, the direct effect of fire was stronger relative to the indirect effects of fire through the vegetation characteristics (Table 3). Habitat-specialist butterfly abundance and richness, unlike total abundance and richness, were overall more affected by changes in vegetation characteristics (Table 3). This result suggests that the correlation between time since burn and habitat-specialist butterfly abundance and richness arises from the effects of fire on vegetation, which in turn influence butterfly responses. Of these variables, habitat-specialist butterfly abundance and richness were most influenced by the amount of bare ground present at a site (Tables 2, 3).

When we examined individual species models, similar patterns emerged in the relative strength of direct and indirect effects (Table 3). For the habitat-specialist species *C. pegala*, the indirect effects were stronger than the direct effect of fire. However, for *S. idalia*, the direct and indirect

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Table 2 Standardized path coefficients and r^2 values from multiple linear regressions with all variables and time since burn. Standardized path coefficients less than 0.01 are listed as 0. Independent variables chosen for inclusion in the path models are: Floral resources (number of flowering ramets), warm-season grass (percent cover of warm-season grasses), and bare ground (percent cover of bare ground)

Dependent variable	Independent variables	Standardized path coefficient	Model r^2
Total butterfly richness	Floral resources	0.12*	0.09**
	Warm-season grasses	0.23***	
	Bare ground	−0.04	
Habitat-specialist butterfly richness	Floral resources	0.11	0.11*
	Warm-season grasses	0.13*	
	Bare ground	−0.24**	
Total butterfly abundance	Floral resources	0.13	0.20***
	Warm-season grasses	0.10	
	Bare ground	−0.28***	
Habitat-specialist butterfly abundance	Floral resources	0.04	0.21***
	Warm-season grasses	0.09	
	Bare ground	−0.35***	
Habitat-specialist species			
Cercyonis pegala	Floral resources	0.04	0.14***
	Warm-season grasses	0.08	
	Bare ground	−0.33***	
Hesperia ottoe	Floral resources	0.11*	0.05*
	Warm-season grasses	0.18**	
	Bare ground	−0.03	
Speyeria cybele	Floral resources	−0.10*	0.06*
	Warm-season grasses	−0.01	
	Bare ground	0.03	
Speyeria idalia	Floral resources	0.14*	0.12**
	Warm-season grasses	0.09	
	Bare ground	−0.23*	
Habitat-generalist Species			
Colias eurytheme	Floral resources	0.17**	0.16**
	Warm-season grass	−0.16*	
	Bare ground	−0.10	
Euptoieta claudia	Floral resources	0.31***	0.15*
	Warm-season Grasses	0.12	
	Bare Ground	0.24*	
Pieris rapae	Floral Resources	0.08	0.11*
	Warm-season Grasses	0.11	
	Bare Ground	0.08	

* Significant at $P < 0.05$ level, ** significant at $P < 0.001$ level, *** significant at $P < 0.0001$ level

effects are equally important (Table 3). For both species, the percent cover of bare ground was the strongest predictor of abundance (Tables 2, 3). For the other two habitat-specialist species, *H. ottoe* and *S. cybele*, the direct effects of fire were a stronger predictor of abundance than the indirect effects (Table 3). For habitat-generalist species (*C. eurytheme* and *P. rapae*), abundance was more influenced by the direct effect of fire than by indirect changes in vegetation (Table 3). However, for *E. claudia*, the indirect effects were stronger. In particular, floral resource availability was the best predictor of abundance (Tables 2, 3).

Discussion

The vegetation components we measured responded to time since burn, as we had predicted, with very few exceptions. In particular, floral resource availability had a

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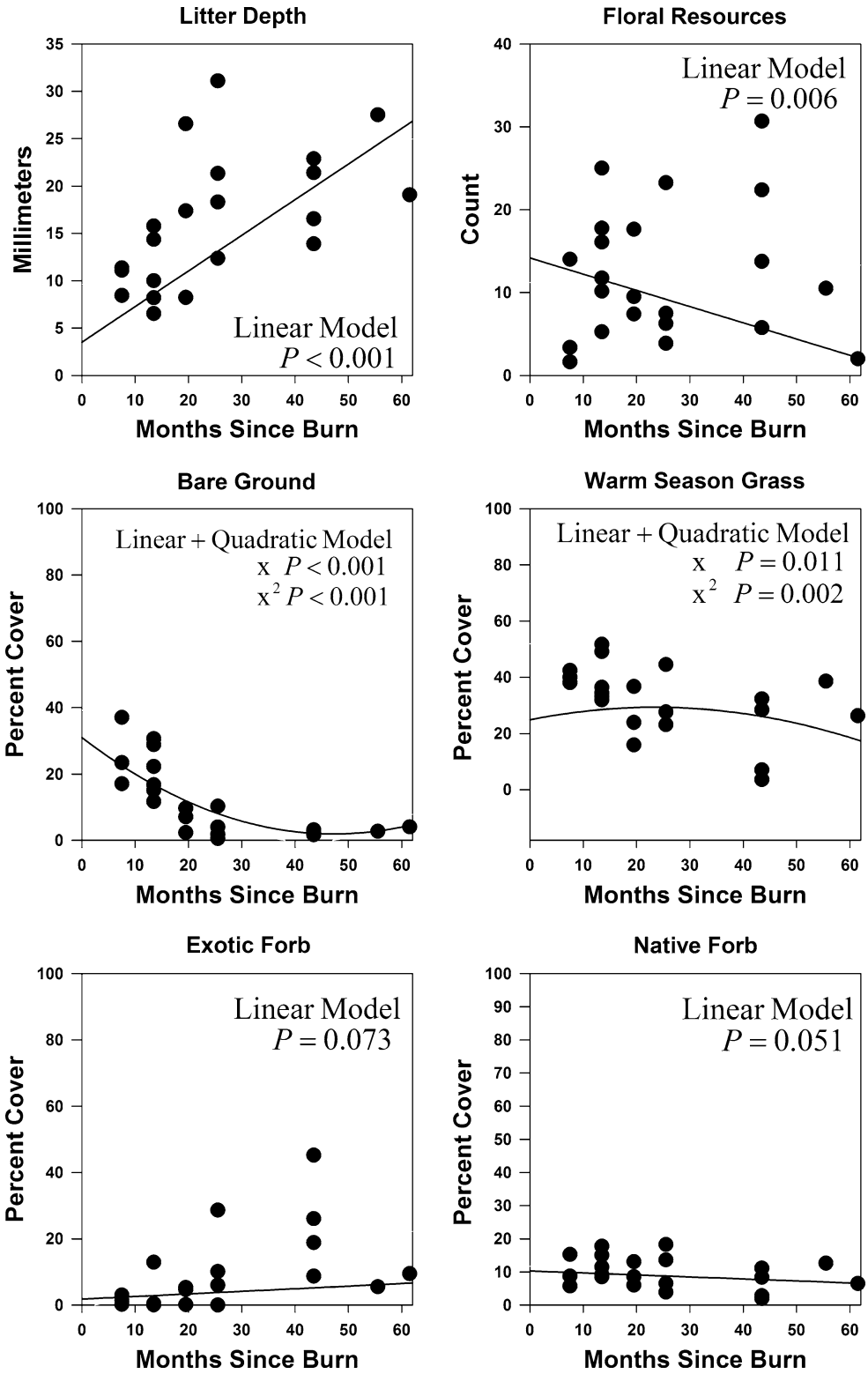

Fig. 3 Repeated measures regressions of vegetation variables with time since burn for remnant tallgrass prairie sites surveyed during 2004 and 2005 and managed with prescribed fire. Vegetation variables were averaged for each management unit. Regression models included both a linear term and a quadratic term. When the quadratic term in the model was significant ($P < 0.05$), indicating that a linear term alone was not sufficient to explain the relationship, models presented include both the linear and quadratic terms. All sites were located in the Loess Hills of western Plymouth County, Iowa, USA

strong negative relationship with time since burn. Flowering activity in forbs has been shown to increase following fire (Ehrenreich and Aikman 1963; Pemble et al. 1981) and we expected that there would be significantly more flowering ramets in our surveys in recently burned areas.

Although most of the vegetation components responded in predictable ways to time since burn, it is interesting that the relationship with bare ground was not linear. Areas surveyed immediately after a fire had high percentages of bare ground throughout the first growing season because

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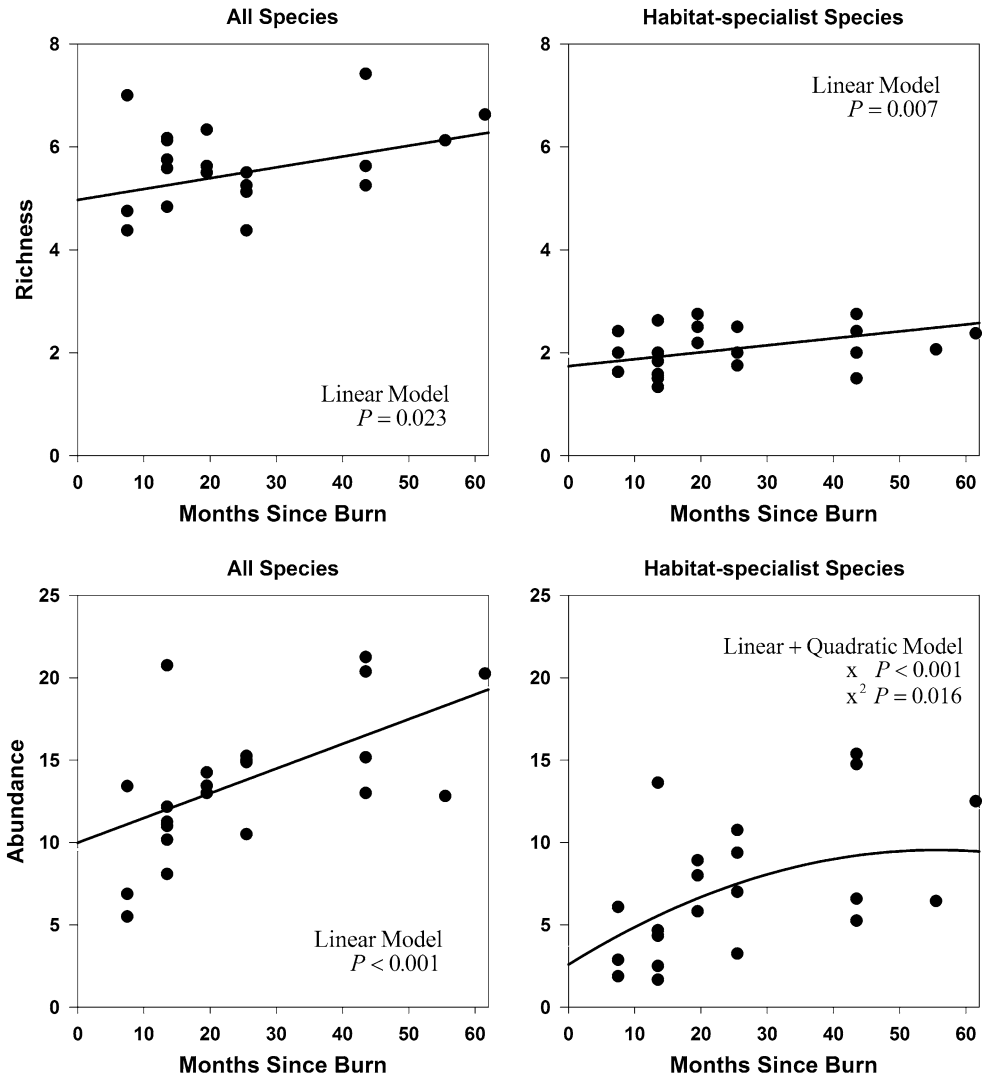

Fig. 4 Repeated measures regressions between time since burn and butterfly abundance/richness for remnant tallgrass prairie sites surveyed during 2004 and 2005 and managed with prescribed fire. Butterfly responses (abundance) were averaged for each management unit. Regression models included both a linear term and a quadratic term. When the quadratic term in the model was significant ($P < 0.05$), indicating that a linear term alone was not sufficient to explain the relationship, models presented include both the linear and quadratic terms. All sites were located in the Loess Hills of western Plymouth County, Iowa, USA

litter accumulation had been consumed by the fire. After 1 year, the percent cover of bare ground was dramatically reduced with the addition of litter accumulated during the first growing season as well as lush re-growth covering bare areas. By the end of the second growing season, the amount of bare ground exposed appeared to level off.

Relatively few studies have documented recovery times for invertebrate or vertebrate species after a prescribed burn, nor have they evaluated the relationships between species abundance in tallgrass prairie and time since burn. Those that have examined these relationships have generally predicted recovery times of 1–5 years post burn (Kaufman et al. 1990; Swengel 1996; Panzer 2002). For example, Kaufman et al. (1990) hypothesized that small mammal species on Konza Prairie, Kansas, differ in response to fire (measured here in density) based on their level of sensitivity (fire-neutral, fire-negative, or fire-positive). They suggested that fire-negative species may have low densities immediately following a fire, followed by steady increases over the next 5 years. Moreover, they proposed the recovery time for fire-negative species ranged from 1–5 years, with densities returning to pre-fire levels. Further evidence for this trend comes from a study by Swengel (1996) on grassland butterflies, which found specialist species declined immediately following a burn and that the effects were evident for 3–5 years after the fire. This proposed scenario for post-fire recovery of fire-negative species is similar to some of the relationships that we found for grassland butterflies. However, our data on butterfly abundances do not appear to consistently level off after 5 years (60 months), suggesting that recovery times for some species may be longer than previously documented. Only for habitat-specialist butterfly abundance and for the habitat-specialist, *C. pegala*, does a recovery time of 5 years appear to fit our data. And, because *C. pegala* was the most abundant habitat-specialist we encountered, the pattern of overall habitat-specialist butterfly recovery time can likely be attributed to the influence of this species.

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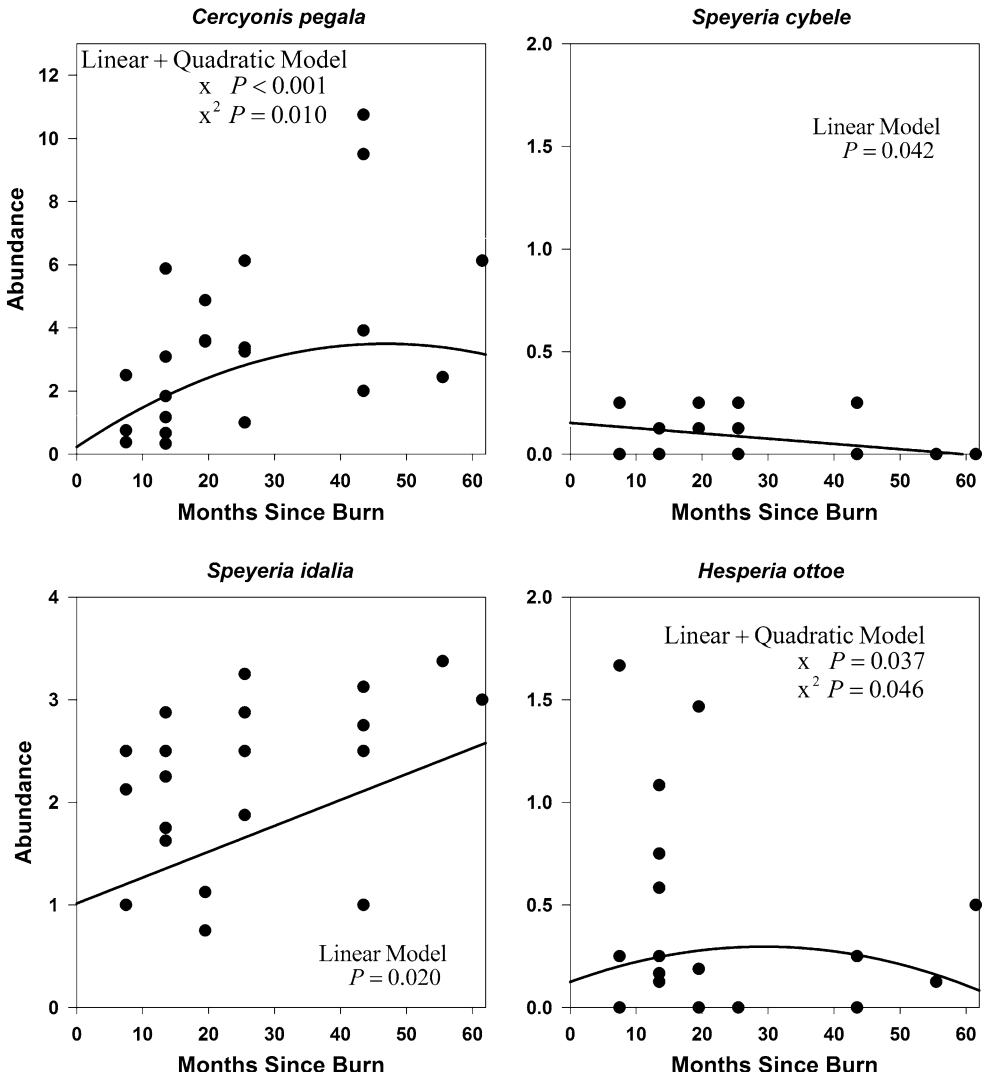

Fig. 5 Repeated measures regressions between time since burn and butterfly abundance/richness for remnant tallgrass prairie sites surveyed during 2004 and 2005 and managed with prescribed fire. Butterfly responses (abundance) were averaged for each management unit. Regression models included both a linear term and a quadratic term. When the quadratic term in the model was significant ($P < 0.05$), indicating that a linear term alone was not sufficient to explain the relationship, models presented include both the linear and quadratic terms. All sites were located in the Loess Hills of western Plymouth County, Iowa, USA

For other species in our dataset, including *S. idalia*, *C. eurytheme*, and *P. rapae*, recovery time appeared to be greater than 50 months. We suspect that if our sites remained unburned for a longer period, we would see a similar leveling off and subsequent decline of butterfly abundance as time since burn increased. For one species, *H. ottoe*, we observed a recovery time of approximately 30 months. It remains to be seen whether this result and others can be generalized to prairie remnants with different spatial configurations, degrees of isolation, or levels of grazing pressure.

In contrast to our findings, Rudolph et al. (2006) found total butterfly abundance in open woodlands was highest in the first growing season following a prescribed fire and decreased thereafter. A similar pattern was observed for the availability of floral resources (Rudolph et al. 2006). However, the abundance of two fritillary species (*Speyeria diana* and *S. cybele*) in this open woodland system was highest 2 years post-burn (Rudolph et al. 2006). Our data for *S. cybele* may have a similar pattern, with peak abundance at 12–24 months post-burn and a decline thereafter.

Using Path Analysis allowed us to decompose the correlations between time since burn and butterfly abundance and to determine the relative contributions of direct and indirect effects. Our findings illustrate the importance of certain habitat features, such as bare ground, on butterfly abundance. For example, *S. idalia* is considered to be a fire-sensitive grassland butterfly species (Huebschman and Bragg 2000; Beilfuss and Harrington 2001) because it exists in dormant stages when most prescribed burns are conducted. In addition to the direct mortality of fire on *S. idalia* eggs and larvae, it is possible that microclimate conditions influence survival (Kopper et al. 2000). Our data indicate that the effects of fire could be acting on *S. idalia* abundance indirectly through changes in the litter layer and exposure of soil surfaces (bare ground). In fact, higher temperatures on sunlit patches of bare ground could prove lethal for *S. idalia* larvae (Kopper et al. 2000). The absence

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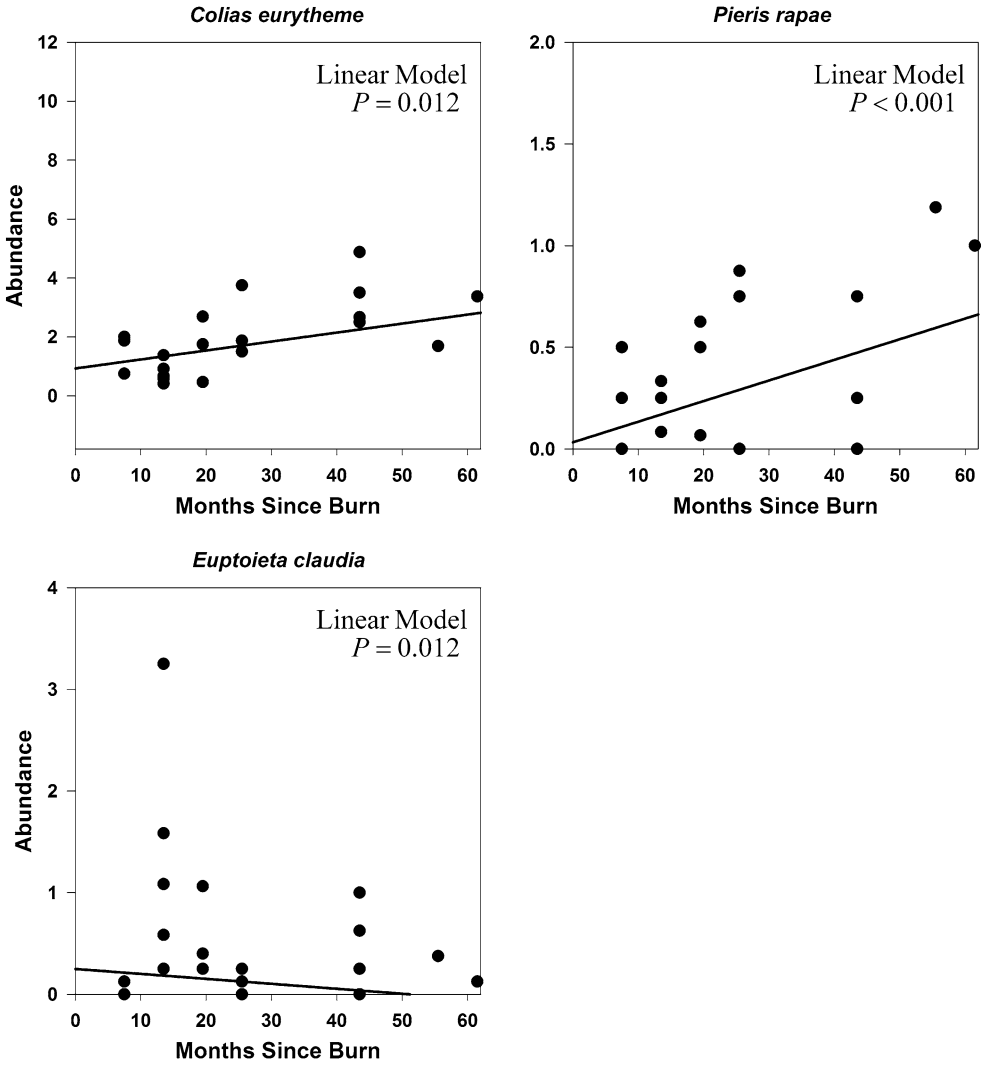

Fig. 6 Repeated measures regressions between time since burn and butterfly richness/abundance for remnant tallgrass prairie sites surveyed during 2004 and 2005 and managed with prescribed fire. Butterfly responses (richness/abundance) were averaged for each management unit. Regression models included both a linear term and a quadratic term. When the quadratic term in the model was significant ($P < 0.05$), indicating that a linear term alone was not sufficient to explain the relationship, models presented include both the linear and quadratic terms. All sites were located in the Loess Hills of western Plymouth County, Iowa, USA

of an insulating litter layer during harsh winters when larvae are dormant could similarly be detrimental to survival. For a species of conservation concern like *S. idalia*, it is important to understand these components of larval survival.

For fire-sensitive butterfly species, some have proposed the only hope for persistence in areas that are burned is in recolonization from nearby unburned areas. Swengel (1996) observed that larger, more vagile prairie-specialists, like *S. idalia*, were more abundant (among habitat-specialist species) in areas that were recently burned. Smaller habitat-specialist species tended to have the lowest abundance in those same areas, presumably because they are less vagile. However, Selby (1992) noted that *S. idalia* and *H. ottoe* movement distances were similar on Five Ridge Prairie. Distances moved by *H. ottoe* ranged between 7 and 1,774 m and distances for *S. idalia* were between 18 and 1,515 m, allowing for recolonization on this site by both species (Selby 1992). We did not examine vagility or size-based recolonization differences among species because abundances of smaller species were rarely high enough to be included in our analyses. However, future researchers may wish to examine this issue.

Recovery times for butterfly populations after prescribed fires in our study are potentially longer than those previously reported. Because fire return intervals on managed prairie remnants are often less than 5 years due to the need for managing woody vegetation, information on recovery times for habitat-specialist insect species is of great importance to managers. Differences in the recovery rates among butterfly species in this study may result from species-specific differences in the relationships between patch size and dispersal distances. Further examination of how landscape configuration and patch size relates to recovery rates may allow managers to refine estimates of recovery rates for local populations of interest. Recovery rates for species of particular interest should be examined when planning prescribed fires.

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Table 3 Decomposition of correlations (effect coefficients) between time since burn and each of the six butterfly abundance variables. The path effect is the indirect effect of the pathway from months since burn through the independent variable listed. Path effects are calculated by multiplying the correlation between time since burn and the independent variable in the path by the standardized path coefficient for the independent variable (see Table 1 for correlation matrix and Table 2 for standardized path coefficients). The total indirect effects are summed from all indirect pathways (path effects) in the model. All models include the independent variables Floral (number of flowering ramets), WS grass (percent cover of warm-season grasses), and BG (percent cover of bare ground). Direct and indirect effects sum to the effect coefficient. Path effect of less than 0.01 are listed as 0

Dependent variable	Independent variables	Path effect	Total indirect effect	Direct effect	Effect coefficient
Total butterfly richness	Floral resources	0	−0.02	0.19	0.17
	Warm-season grasses	−0.04			
	Bare ground	0.02			
Habitat-specialist butterfly richness	Floral resources	0	0.12	0.08	0.20
	Warm-season grasses	−0.03			
	Bare ground	0.15			
Total butterfly abundance	Floral resources	0	0.15	0.20	0.35
	Warm-season grasses	−0.02			
	Bare ground	0.17			
Habitat-specialist butterfly abundance	Floral	0	0.20	0.15	0.35
	Warm-season Grasses	−0.02			
	Bare ground	0.22			
Habitat-specialist Species					
Cercyonis pegala	Floral resources	0	0.19	0.07	0.26
	Warm-season grasses	−0.01			
	Bare ground	0.20			
Hesperia ottoe	Floral resources	0	−0.02	−0.07	−0.09
	Warm-season grasses	−0.03			
	Bare ground	0.01			
Speyeria cybele	Floral resources	0	−0.01	−0.21	−0.22
	Warm-season grasses	0			
	Bare ground	−0.01			
Speyeria idalia	Floral resources	−0.01	0.12	0.12	0.24
	Warm-season grasses	−0.02			
	Bare ground	0.15			
Habitat-generalist Species					
Colias eurytheme	Floral resources	−0.01	0.08	0.24	0.32
	Warm-season grasses	0.03			
	Bare ground	0.06			
Euptoieta claudia	Floral resources	−0.01	−0.18	0.04	−0.14
	Warm-season grasses	−0.02			
	Bare ground	−0.15			
Pieris rapae	Floral resources	0	−0.08	0.38	0.30
	Warm-season grasses	−0.02			
	Bare ground	−0.06			

For habitat-specialist species, path models highlighted the importance of the indirect effects of fire on habitat features (such as increases in the cover of bare ground) and quantified how these indirect effects may influence butterfly abundance after a fire. Our results clearly demonstrate that both the direct and indirect effects of fire should be considered in the management and conservation of native butterfly species. The indirect effects of fire affect post-fire recovery times and warrant further consideration.

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Appendix A

See Table 4.

Table 4 List of all butterfly species found in study area during 2004 and 2005

Species name	Common name	Category	Abundance	Pop. trend in Iowa
Family Papilinidae				
Papilio polyxenes	Black Swallowtail	Habitat-generalist	7	C, S
Papilio cresphontes	Giant Swallowtail	Woodland	14	U, UK
Papilio glaucus	Eastern Tiger Swallowtail	Woodland	63	C, S
Family Pieridae				
Colias eurytheme	Orange Sulfur[a]	Habitat-generalist	368	C, UK
Colias philodice	Clouded Sulfur	Habitat-generalist	3	C, UK
Eurema lisa	Little Yellow	Habitat-generalist	1	LC, UK
Pieris rapae	Cabbage White[a]	Habitat-generalist	86	C, S
Pontia protodice	Checkered White	Habitat-generalist	4	C, UK
Family Nymphalidae				
Danaus plexippus	Monarch[a]	Habitat-generalist	46	C, UK
Megisto cymela	Little Wood Satyr	Habitat-generalist	157	C, UK
Cercyonis pegala	Common Wood Nymph[a]	Habitat-specialist	689	C, UK
Asterocampa celtis	Hackberry Emperor	Woodland	6	C, UK
Limenitis arthemis	Red-spotted Purple	Woodland	5	LC, UK
Limenitis archippus	Viceroy	Habitat-specialist	3	C, UK
Junonia coenia	Common Buckeye	Habitat-generalist	5	C, S
Vanessa atalanta	Red Admiral[a]	Habitat-generalist	44	C, S
Vanessa cardui	Painted Lady	Habitat-generalist	36	C, S
Vanessa virginiensis	American Lady	Habitat-generalist	2	C, UK
Polygonia comma	Eastern Comma	Woodland	1	C, UK
Chlosyne gorgone	Gorgone Checkerspot	Habitat-generalist	4	LC, UK
Phyciodes tharos	Pearl Crescent	Habitat-generalist	10	C, UK
Boloria bellona	Meadow Fritillary	Habitat-specialist	1	LC, UK
Speyeria aphrodite	Aphrodite Fritillary	Habitat-specialist	1	LC, UK
Speyeria cybele	Great Spangled Fritillary[a]	Habitat-specialist	41	C, UK
Speyeria idalia	Regal Fritillary[a]	Habitat-specialist	397	R, D
Euptoieta claudia	Variegated Fritillary[a]	Habitat-generalist	148	LC, UK
Family Lycaenidae				
Satyrium titus	Coral Hairstreak	Habitat-specialist	13	C, UK
Callophrys gryneus	Olive Hairstreak	Habitat-generalist	4	LC, UK
Strymon melinus	Gray Hairstreak[a]	Habitat-generalist	87	C, UK
Lycaena hyllus	Bronze Copper	Habitat-specialist	1	C, UK
Lycaena dione	Gray Copper	Habitat-specialist	11	LC, UK
Everes comyntas	Eastern Tailed Blue[a]	Habitat-generalist	111	C, UK
Celastrina ladon	Spring Azure	Habitat-generalist	12	C, UK
Celastrina neglecta	Summer Azure	Habitat-generalist	47	C, UK
Lycaeides melissa	Melissa Blue	Habitat-generalist	6	LC, UK
Echinargus isola	Reakirt's Blue[a]	Habitat-generalist	57	C, UK
Family Hesperiidae				
Hesperia ottoe	Ottoe Skipper[a]	Habitat-specialist	91	U, UK
Polites peckius	Peck's Skipper	Habitat-generalist	8	LC, UK
Polites mystic	Long Dash	Habitat-specialist	8	LC, UK

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Table 4 continued

Species name	Common name	Category	Abundance	Pop. trend in Iowa
Polites themistocles	Tawny-edged Skipper[a]	Habitat-generalist	43	C, UK
Polites origenes	Crossline Skipper	Habitat-specialist	16	LC, UK
Atalopedes campestris	Sachem	Habitat-generalist	9	LC, UK
Anatrytone logan	Delaware Skipper	Habitat-specialist	18	LC, UK
Poanes hobomok	Hobomok Skipper	Habitat-generalist	1	C, UK
Atrytonopsis hianna	Dusted Skipper	Habitat-specialist	6	U, UK
Lerodea eufala	Eufala Skipper	Habitat-generalist	1	LC, UK
Thorybes pylades	Northern Cloudywing	Habitat-specialist	13	LC, UK
Erynnis horatius	Horace's Duskywing[a]	Habitat-specialist	66	LC, UK
Pyrgus communis	Common-checkered Skipper	Habitat-generalist	8	LC, UK

Butterfly abundance is summed across rounds and years. Butterflies are divided into categories based on their requirements for host plants and floral resources. Information is given on the population trends for each species in Iowa based on the Iowa Wildlife Action Plan (IDNR 2006). The first letter represents the overall abundance of the species in Iowa (*C* common, *LC* locally common, *U* uncommon, *R* rare). The second letter in the column represents the population trend of the species in Iowa (*UK* unknown, *S* stable, *D* decreasing). All sites are located in the Loess Hills of western Plymouth County, Iowa, USA

[a] Species with at least 20 individuals and present on at least 40% of study sites

Appendix B

See Table 5.

Table 5 Burn history and area of Loess Hills, Iowa management units

Unit name	Management type	Unit area (ha)	Year							
			1997	1998	1999	2000	2001	2002	2003	2004
12	Burned	10						X		
13	Burned	58				X			X	X
15	Burned	73				X			X	
S2	Burned	10				X			X	
Z	Burned	10					X			X
R4	Burned	56							X	X
JC	Burned	102					X			
R2	Burned	41					X			X
R5	Burned	64							X	
R3	Burned	62							X	X
1	Burned & grazed	44					X			
2	Burned & grazed	11					X			
3–4	Burned & grazed	60					X			
5	Burned & grazed	21		X		X		X		
6	Burned & grazed	59				X				
7	Burned & grazed	20	X	X		X		X		
8	Burned & grazed	27			X					
9	Burned & grazed	64			X		X			
10	Burned & grazed	26						X	X	X
11	Burned & grazed	31						X		
B1	Burned & grazed	63							X	
B2	Burned & grazed	20							X	

An X in the column for a particular year indicates that a prescribed burn was conducted. Study sites include Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land

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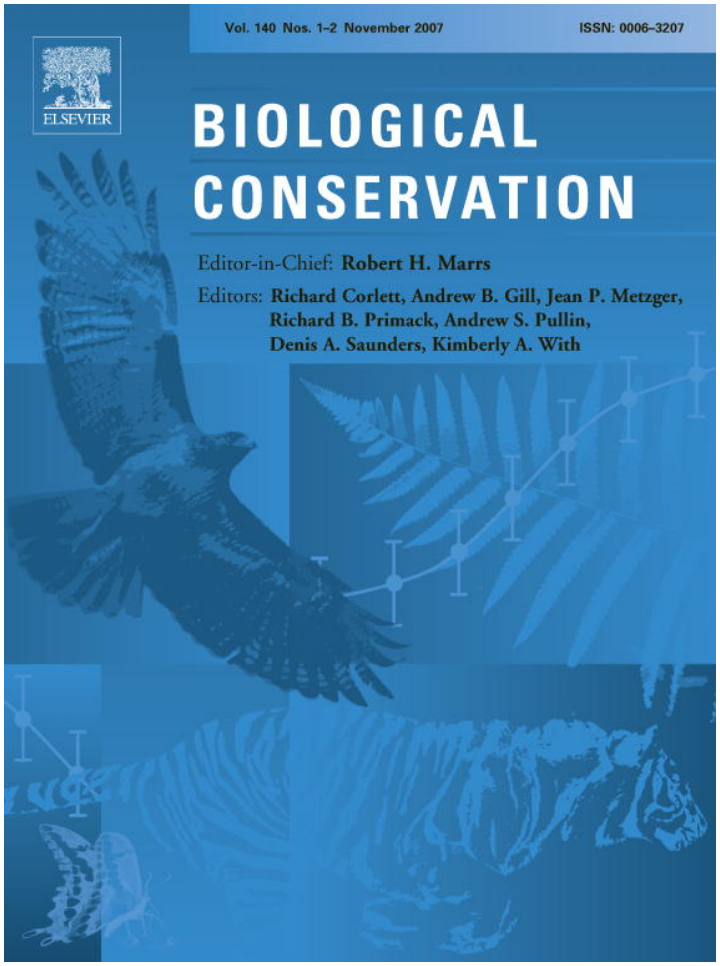

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Butterfly responses to prairie restoration through fire and grazing

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ABSTRACT

The development of land for modern agriculture has resulted in losses of native prairie habitat. The small, isolated patches of prairie habitat that remain are threatened by fire suppression, overgrazing, and invasion by non-native species. We evaluated the effects of three restoration practices (grazing only, burning only, and burning and grazing) on the vegetation characteristics and butterfly communities of remnant prairies. Total butterfly abundance was highest on prairies that were managed with burning and grazing and lowest on those that were only burned. Butterfly species richness did not differ among any of the restoration practices. Butterfly species diversity was highest on sites that were only burned. Responses of individual butterfly species to restoration practices were highly variable. In the best predictive regression model, total butterfly abundance was negatively associated with the percent cover of bare ground and positively associated with the percent cover of forbs. Canonical correspondence analysis revealed that sites with burned only and grazed only practices could be separated based on their butterfly community composition. Butterfly communities in each of the three restoration practices are equally species rich but different practices yield compositionally different butterfly communities. Because of this variation in butterfly species responses to different restoration practices, there is no single practice that will benefit all species or even all species within habitat-specialist or habitat-generalist habitat guilds.

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1. Introduction

Destruction of habitat is the most prevalent threat to butterfly and insect populations around the world (New et al., 1995). Habitat losses across the globe have resulted from the conversion of land for agriculture and development (Saunders et al., 1991; Stoner and Joern, 2004). Grassland ecosystems are especially vulnerable to losses from agricultural development and, in fact, the tallgrass prairie region of North America is one of the most endangered ecosystems on Earth (Smith, 1981; Noss et al., 1995). Given these extensive losses of habitat, the preservation of remaining habitat is of great concern. Overall conservation strategies should not only include preservation of existing habitat but also habitat restoration (Jordan, 1997).

In addition to habitat loss, grassland ecosystems have been degraded by the disruption of their natural disturbance regimes. Studies of butterflies and insects from different regions of the globe have indicated that populations respond differently to disturbances and that many species have different habitat requirements at each life stage (New et al., 1995;

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Samways, 2007). In North American grasslands, as in grasslands around the world, methods used to restore habitats have included reintroducing natural disturbances such as fire and grazing.

The effects of grazing on butterflies may be moderated by the effects of grazing on their host plants. Long term studies of the skipper *Hesperia comma* in the UK have illustrated how grazing influences their grass host plant, *Festuca ovina* (Thomas et al., 1986; New, 1997). Over time, reduced grazing led to taller host plants and reduced oviposition site suitability for the species. A more recent reintroduction of grazing in the area has returned many areas to suitable habitat for *H. comma* (Thomas et al., 1986; New, 1997). Another European grassland butterfly, *Lysandra bellargus*, had larger populations on sites where grazing kept vegetation height between 1 cm and 4 cm (Thomas, 1983). In contrast, studies of many other European grassland butterflies have indicated that species richness tends to be higher where vegetation is taller from reduced disturbance intensity (Ockinger et al., 2006; Poyry et al., 2006). For one threatened butterfly in Belgium, the bog fritillary (*Procossiana eunomia*), grazing decreased butterfly populations by an estimated 74% compared to un-grazed sites (Schtickzelle et al., 2007). Differences in microclimate requirements in conjunction with the relatively small sizes of remaining habitat patches have led to the implementation of single species management in order to preserve rare insects and butterflies.

Large grazing mammals were present throughout the evolutionary history of North American prairies and are an important component of the ecosystem (Mutel, 1989). Grazing can increase plant species diversity when used in a moderate grazing regime (Soleki and Toney, 1986). Intensive grazing could have negative effects on sensitive invertebrate species (Moffat and McPhillips, 1993; Swengel and Swengel, 1999) and many prairies have likely been destroyed or degraded by improper grazing regimes (Williams, 1997).

Fire is an important component of many ecosystems around the world (Sauer, 1950; Huntzinger, 2003; Fleishman, 2000; Vieira et al., 1996) and of grassland ecosystems in particular (Collins and Gibson, 1990; Schultz and Crone, 1998). Following a period of suppression, fire has increasingly been used as a management tool for restoring native habitats (Panzer and Schwartz, 2000; Huntzinger, 2003; Hobbs and Atkins, 1990). However, some researchers have expressed concern about the response of insect species to prescribed fire in small, isolated remnants (Dana, 1991; Swengel, 1996; Panzer, 2002; Samways, 2007). Local populations of insects on fragmented preserves may not survive repeated prescribed burns (Panzer, 2002).

In the state of Iowa, USA, less than 0.01% of the original 12 million hectares of prairie remains (Sampson and Knopf, 1994). As a result, the landscape is highly fragmented with small, isolated remnants surrounded by a matrix of agricultural lands. The negative consequences of habitat fragmentation on plants and animals are numerous and have been studied extensively (e.g., Kruess and Tscharntke, 1994; Quinn, 2004; Wilsey et al., 2005; Benedick et al., 2006; Cagnolo et al., 2006). Because smaller fragments have a higher edge-to-area ratio than larger fragments (Webb, 1989; Kiviniemi and Eriksson, 2002; Benedick et al., 2006), they are more susceptible to invasion by non-native species (e.g., Kiviniemi and Eriksson, 2002; Hansen and Clevenger, 2005). In fact, invasive species such as leafy spurge (*Euphorbia esula*) and smooth brome (*Bromus inermis*) are a major threat to biodiversity in the remaining prairies of North America (Fellows and Newton, 1999; Vinton and Goergen, 2006).

The Loess Hills of western Iowa contain some the state's largest unplowed native prairies. This unique landform is composed of fine soil particles, or loess, deposited by wind that has blown over glacial melt-water silt from the Missouri River bottoms (Mutel, 1989). Many of the remaining prairies in the Loess Hills have historically been used as pastures and hay meadows (Mutel, 1989). Remnant prairies in the Loess Hills area are home to almost 100 species of butterflies (Orwig, 1990), including some rare and endangered species. The diversity of butterflies in the state of Iowa has been declining because of habitat destruction and alteration (Schlicht and Orwig, 1998). The invertebrate communities of tallgrass prairies make up a large component of the total biodiversity in the ecosystem and their survival is an important issue for conservation (Dietrich, 1998; Schlicht and Orwig, 1998).

The questions addressed in this study are:

1. How do grazing and burning restoration practices affect butterfly species richness and abundance on prairie remnants managed for biological diversity?
2. Are there distinct butterfly communities associated with burned only, grazed only, or burned and grazed restoration practices?
3. How has the vegetation responded to prescribed restoration practices and how have butterflies responded to the vegetation?

2. Methods

2.1. Study area

We conducted butterfly surveys on prairie remnants located in Plymouth County, Iowa, USA at the northern end of the Loess Hills Landform (Fig. 1). Specifically, survey sites were located on Broken Kettle Grasslands Preserve (more than 1800 ha, owned and managed by The Nature Conservancy), Five Ridge Prairie (approximately 320 ha, owned and managed by the Plymouth County Conservation Board), and on adjacent private land.

We surveyed a total of 69 sites located within 28 management units. The study area was divided into units based on the restoration practices (burned only, grazed only, or burned and grazed) they received. Management units ranged in size from approximately 10 to over 100 ha, with an average size of 40 ha (Appendix A). Burned units were managed with prescribed fires conducted during the fall and spring in 2–6 year rotations (Appendix A). Prescribed burns conducted within a management unit were designed to burn the entire area within that unit. The limited number of burned only units available ($n = 10$) restricted our ability to further divide units into categories by season or frequency of burn. Grazed units received light rotational grazing by domestic cattle with stocking rates of approximately one cow–calf pair (one Animal

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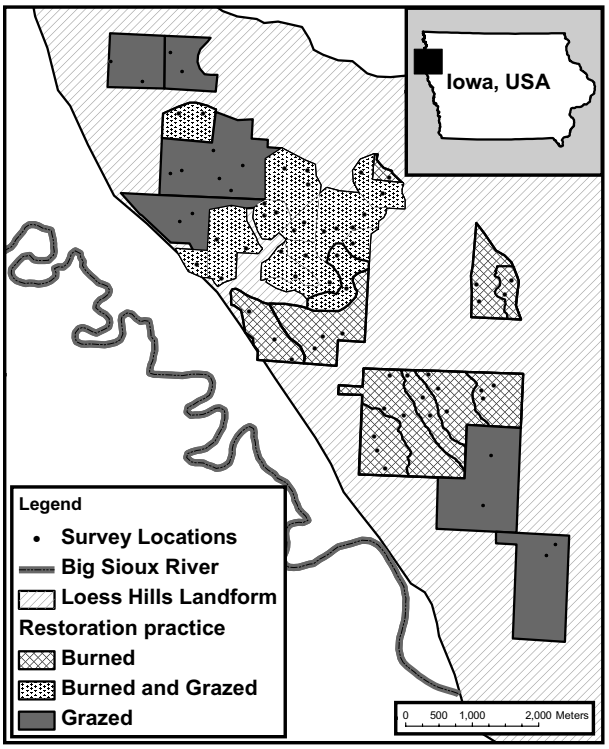

Fig. 1 – Map of study sites with restoration practices, management unit boundaries, and butterfly survey locations. All sites are located in Plymouth County, IA, USA. Study sites include Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land.

Unit) per four ha (Scott Moats, Director of Stewardship, Iowa Chapter of The Nature Conservancy, personal communication). Grazing in this system is used as an ecological management tool and grazing intensity was much lighter than in a system where grazing is primarily for economic gain. Present restoration practices have been in place at the study area for a minimum of 4 years. We placed survey sites randomly with the restrictions that they were at least 150 m apart and at least 50 m from any unit edge or woody edge. We established at least two survey plots in most of the management units. However, for some management units, size prevented the placement of more than one survey site using the above restrictions. Using the above sampling design, there were 16 survey sites in six grazed only units, 26 survey sites in 10 burned only units, and 27 survey sites in 12 burned and grazed units for a total sample size of 28 management units (Fig. 1).

2.2. *Butterfly surveys*

We conducted two rounds of butterfly surveys each year between 1 June and 15 August of 2004 and 2005. We conducted surveys on warm (21–35 °C), sunny (less than 50% cloud cover), and calm (winds less than 16 km/h) days between 10:00 h and 18:30 h. We recorded weather conditions (temperature, cloud cover, and wind speed) and time of day prior to beginning a survey. We surveyed butterflies in 50 m × 50 m plots at each survey site. Surveys consisted of two observers walking through a plot in a zig-zag pattern while netting individuals observed for 30 min (e.g., Debinski and Brussard, 1994). We placed netted butterflies in glassine envelopes to avoid double counting of individuals. At the end of the survey, we recorded data for each individual, including the species name, activity at the time of capture, and sex (if known). We released all butterflies at the completion of the survey unless their identity could not be confirmed. Unidentified individuals were collected as voucher specimens to be identified in the lab and are housed in D.M. Debinski's laboratory at Iowa State University, Ames, IA, USA.

2.3. *Vegetation and floral resource surveys*

We measured the vegetation at each survey site twice each year in June and July of 2004 and 2005. Variables included vegetation height, litter depth, percent cover of warm season grasses, percent cover of cool season grasses, percent cover of native forbs, percent cover of exotic forbs, percent shrub cover, percent cover of litter, and percent cover of bare ground. Most of the cool season grasses in the study area were one of two exotic species, smooth brome (*B. inermis*) and Kentucky bluegrass (*Poa pratensis*). All of the warm season grasses in the study area were native species. The most commonly occurring warm season grasses included big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schisachyrium scoparium*), and side oats grama (*Bouteloua curtipendula*). We measured vegetation height in dm using a Robel pole and a modified version of the Robel method (Robel et al., 1970) at 5 m and 25 m from the center of the 50 m × 50 m plot in each cardinal direction. Similarly, we measured litter depth in mm using a ruler at 5 m and 25m from the center of the plot in each cardinal direction. We measured the percent cover variables by placing a 0.5 m × 0.5 m Daubenmire frame (Daubenmire, 1959) on the ground at locations 5 m and 25 m away from the center of the plot in each cardinal direction. We determined the percent cover of each vegetation type visually within the sampling frame. For all of the vegetation variables, we averaged the measurements taken at each of the 8 locations within a plot for each survey site.

Immediately following each butterfly survey, we conducted a floral resource survey on each plot to assess the availability of floral resources. One observer walked a one-half meter wide transect diagonally across the survey plot counting the number of flowering ramets of all nectar species within the transect.

2.4. *Data analysis*

We categorized butterflies into three habitat guilds (habitat-specialists, habitat-generalists, and woodland species) based on their requirements for host plant and floral resources (Appendix B). We considered a species to be a habitat-specialist if it relies on a native prairie plant species for either its larval food or adult nectar resources. As a result, habitat-specialist species are found primarily in high quality prairie habitat. We considered a species to be a habitat-generalist if it did not require a native prairie plant species for either its larval food or adult nectar resources. As a result of this cate-

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gorization, species we considered to be habitat-generalists use a variety of common plant species (both non-prairie natives and non-natives). Habitat-generalist species are found in a wide variety of open habitats including yards, roadsides, and disturbed areas. Butterfly species that we categorized as woodland species utilize woodland plant species for their host and floral resources. Habitat-specialist species correspond to the "habitat-sensitive" category and habitat-generalist species correspond to the "disturbance-tolerant" category of Ries et al. (2001) and Reeder et al. (2005). Previous uses of the term "disturbance-tolerant" referred to disturbances such as removal of native habitat. We changed the terminology here to prevent misinterpretation of the word "disturbance." Only species in the habitat-specialist and habitat-generalist guilds were included in the analyses.

We compared butterfly species richness, abundance, and diversity (Shannon Diversity Index) among the three restoration practices (burned only, grazed only, and burned and grazed) using Analysis of Variance (ANOVA) in SAS v8.2 (SAS Institute, 1999). For each of these three response variables, we tested a model that included restoration practice as a fixed effect and community type (habitat-specialist vs. habitat-generalist) as a repeated measurement at each site. We also included a term in the model to test for an interaction between restoration practice and community type. Butterfly data were summed over the two rounds for each survey site, averaged for sites within each management unit, and averaged over the 2 years creating an overall average for each management unit ($N = 28$). Abundance data were log transformed when necessary to improve the normality of their distributions. For species that had a total abundance of greater than 50 individuals summed across all sites over both years and were present on at least 40% of all sites, ANOVAs were conducted to test for differences in their abundance among the three restoration practices. Pairwise comparisons were made between practices using Tukey–Kramer adjustments for multiple testing.

To determine whether local vegetation characteristics differed among the restoration practices, we performed ANOVAs for each of the measured vegetation variables. Pairwise comparisons were made between practices using Tukey–Kramer adjustments for multiple testing. Percent cover vegetation variables were arcsin transformed prior to analyses. All local vegetation variables were entered into stepwise linear regressions to determine which of them were important in explaining butterfly species richness and abundance on our sites. A significance level of 0.05 was required to enter into any vegetation model. Models were formed for each of the butterfly community response variables (abundance, species richness, and species diversity). For the most abundant butterfly species, individual species responses to local vegetation characteristics were examined using linear regressions of the mean abundance of each species with the environmental variables.

We used canonical correspondence analysis (CCA) to assess the differences in butterfly species composition among sites and to examine the relationships among the environmental variables and both butterfly species composition and restoration practice (R Development Core Team, 2004). Differences in community composition are represented as the physical distance in two dimensions (CCA1 and CCA2) of each site with respect to the others on the plot. Sites that are near one another have more similar butterfly species compositions than sites that are more distant. The analysis is constrained by environmental variables measured for each site which are indicated with arrows that represent the direction and strength (length of arrow) of their correlations. Prior to analysis, rare species (<10 individuals observed across all sites in both years) were eliminated from the dataset.

We performed a forward stepwise discriminant analysis to determine whether the sites could be classified into a particular restoration practice based on their species composition. Rare species (<10 individuals) were removed prior to analysis. Discriminant analyses were performed using JMP v5.1 (SAS Institute, 2002). Analyses were conducted first using all three restoration practices and then using just the burned only and the grazed only practices.

3. Results

Nearly 4000 individuals of 51 different butterfly species were observed during our surveys in 2004 and 2005. Of the 51 species, 28 were habitat-generalists, 16 were habitat-specialists, and 7 were woodland species (Appendix B). Two habitat-specialist butterfly species, *Speyeria idalia* and *Cercyonis pegala*, and one habitat-generalist species, *Colias eurytheme*, were the most abundant species encountered, making up over 50% of the individuals observed. Three species encountered in the study area (*S. idalia*, *Hesperia ottoe*, and *Atrytonopsis hianna*) are species of conservation concern in the Iowa Department of Natural Resources Draft Conservation Plan (IDNR, 2005).

3.1. *Butterfly responses to restoration practice*

Butterfly abundance differed among the three restoration practices ($F = 8.07$, d.f. = 2, 25, $P = 0.003$, Table 1). The highest mean butterfly abundance occurred in the burned and grazed restoration practice and the lowest in the burned only practice (Table 1). Butterfly species richness did not differ among the three restoration practices ($F = 1.51$, d.f. = 2, 25, $P = 0.226$; Table 1). Butterfly diversity was highest in the burned only restoration practice but did not differ between the grazed only and burned and grazed practices ($F = 7.16$, d.f. = 2, 25, $P = 0.004$; Table 1). Because the P-values for restoration practice by community interactions were greater than 0.05 in all of the above analyses, we did not analyze the habitat-specialist community separately from the habitat-generalist community.

For individual butterfly species, most habitat-generalists did not differ in mean abundance or number of butterflies per hectare among the restoration practices (Table 2). However, the mean abundance of *Danaus plexippus* in the grazed only restoration practice was more than twice the abundance in the burned only practice. In addition, *Colias eurytheme* was less than half as abundant in the burned only restoration practice than in burned and grazed practice. Also, *C. eurytheme* abundance in the burned only practice was less than one third as high as in grazed only.

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Table 1 – Three butterfly community response variables, total butterfly abundance (abundance), total butterfly species richness (species richness), and Shannon Diversity (diversity), tested using ANOVA for differences among the three restoration practices (d.f. = 2, 25)

Butterfly response	Burned		Grazed		Burned and Grazed		F	P
	Mean	SD	Mean	SD	Mean	SD		
Abundance	20.17	6.28a	27.78	5.67ab	31.48	7.25b	7.65	0.003
Species richness	8.64	1.48	7.44	1.78	8.53	1.19	1.44	0.256
Diversity	2.34	0.22a	1.93	0.31b	2.00	0.32b	0.04	0.004

Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

Table 2 – Total number of individuals summed across both years (*n*), average number of butterflies per hectare (*n*/ha) and mean number of butterflies per unit (mean) for 2004 and 2005 occurring in burned, grazed, and burned and grazed restoration practices

Species name	Common name	Burned			Grazed			Burned and Grazed			Total	
		n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*	*P*
Habitat-generalist												
Family Pieridae												
Colias eurytheme	Orange Sulfur	19.20	96	4.80a	64.00	192	16.00b	45.32	272	11.33b	560	0.001
Pieris rapae	Cabbage White	4.40	22	1.10	8.00	24	2.00	10.68	64	2.67	110	0.406
Family Nymphalidae												
Danaus plexippus	Monarch	3.60	18	0.90a	9.00	27	2.25b	4.68	28	1.17ab	73	0.015
Megisto cymela	Little Wood Satyr	8.60	43	2.15	11.00	33	2.75	19.00	114	4.75	190	0.361
Vanessa atalanta	Red Admiral	4.00	20	1.00	2.00	6	0.50	4.00	24	1.00	50	0.593
Euptoieta claudia	Variegated Fritillary	19.80	99	4.95	19.68	59	4.92	8.16	49	2.04	207	0.362
Family Lycaenidae												
Strymon melinus	Gray Hairstreak	13.00	65	3.25	11.32	34	2.83	3.68	22	0.92	121	0.104
Everes comyntas	Eastern Tailed Blue	12.60	63	3.15	7.68	23	1.92	8.00	48	2.00	134	0.528
Echinargus isola	Reakirt's Blue	6.40	32	1.60	2.32	7	0.58	4.16	25	1.04	64	0.574
Family Hesperiidae												
Polites themistocles	Tawny-edged Skipper	5.00	25	1.25	3.00	9	0.75	3.00	18	0.75	52	0.547
Habitat-specialist												
Family Nymphalidae												
Cercyonis pegala	Common Wood Nymph	38.20	191	9.55a	99.68	299	24.92b	83.00	498	20.75b	988	0.021
Speyeria cybele	Great Spangled Fritillary	6.60	33	1.65a	3.32	10	0.83ab	1.32	8	0.33b	51	0.029
Speyeria idalia	Regal Fritillary[a]	22.00	110	5.50a	50.00	150	12.50ab	47.84	287	11.96b	547	0.039
Family Hesperiidae												
Hesperia ottoe	Ottoe Skipper[a]	15.60	78	3.90a	0.68	2	0.17b	2.16	13	0.54b	93	0.002

P-values are given for ANOVA tests for differences among restoration practices for butterfly species (d.f. = 2, 25). Only species with a total abundance of at least 50 individuals and were present on at least 40% of sites are listed. A complete species list is located in Appendix B. Butterflies are separated into habitat-specialist and habitat-generalist habitat guilds based on their habitat requirements for food and host plants.

a Denotes Species of Conservation Concern, Iowa DNR Draft Comprehensive Plan. Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

For habitat-specialists, the responses of individual species were mixed. *C. pegala* was less than half as abundant in the burned only restoration practice than in grazed only or burned and grazed. The abundance of *S. idalia* in the burned only practice was half that of burned and grazed or grazed only. In contrast, the abundance of *Speyeria cybele* was five times higher in the burned only restoration practice than in the burned and grazed practice. *Hesperia ottoe* was more abundant in the burned only practice than in grazed only. We found more than 20 times more individuals of *H. ottoe* in the burned only restoration practice than in grazed only.

3.2. *Vegetation responses to restoration practice*

The vegetation variables we measured had mixed responses with respect to the restoration practices (Table 3). The burned only practice had higher percent cover of both warm season grasses and bare ground and lower percent cover of cool season grasses and lower litter depth and than either of the other two restoration practices (Table 3). The grazed only restoration practice had a higher percent cover of litter than did the burned only or burned and grazed practices (Table 3). The percent cover of all forbs was lower in the burned only

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Table 3 – Environmental variables tested using ANOVA for differences among the three restoration practices (d.f. = 2, 25)

Environmental variable	Burned		Grazed		Burned&Grazed		P
	Mean	SD	Mean	SD	Mean	SD	
Floral resources (# flowering ramets)	9.55	5.30	23.31	16.09	14.32	9.32	0.190
Vegetation height (dm)	2.67	2.15	2.13	0.77	2.55	0.62	0.561
Litter depth (mm)	11.79	7.19a	21.49	7.81b	19.41	4.71b	0.003
Warm season grasses (%)	41.55	6.26a	16.88	10.61b	25.26	11.88b	0.001
Cool season grasses (%)	1.98	2.07a	26.27	9.89b	25.76	11.98b	<0.001
Forb cover (%)	12.69	4.21a	23.18	7.89b	23.01	10.39b	0.008
Native forb (%)	12.13	4.00	10.89	6.45	7.92	4.53	0.133
Exotic forb (%)	0.56	0.95a	12.29	7.10b	15.09	12.45b	<0.001
Shrub (%)	7.05	5.11	2.69	1.48	3.95	3.32	0.064
Litter (%)	15.68	5.08a	25.01	7.35b	17.86	4.83ab	0.013
Bare ground (%)	20.49	10.19a	5.97	5.33b	4.37	3.47b	<0.001

Different letters following means indicate $P < 0.05$ for Tukey–Kramer adjusted pairwise comparisons.

restoration practice than in either of the other two restoration practices. This reduced cover of forbs in the burned only restoration practice was driven by exotic forb cover, which was lower in the burned only practice than in the other two restoration practices (Table 3).

3.3. *Butterfly responses to vegetation*

The abundance of three habitat-generalist butterfly species, *C. eurytheme*, *D. plexippus*, and *Euptoieta claudia*, was positively correlated with floral resources (Table 4). Three species, *H. ottoe*, *Strymon melinus*, and *E. claudia*, had negative associations with litter depth while *S. idalia* and *C. pegala* had positive ones. Total forb cover was positively correlated with just one habitat-generalist species (*C. eurytheme*), but it was negatively correlated with one habitat-specialist species (*H. ottoe*). Species relationships with the percent cover of bare ground were also mixed, two species (*H. ottoe* and *S. melinus*) had positive associations and three species (*C. pegala*, *C. eurytheme*, and *S. idalia*) had negative ones. In addition, warm season grasses and cool season grasses had both positive and negative associations with butterfly species. Species that had positive correlations with cool season grasses (*C. pegala*, *C. eurytheme*, and *D. plexippus*) had negative correlations with warm season grasses and the species (*H. ottoe*) that had a negative correlation with cool season grasses had a positive correlation with warm season grasses. No species had a relationship, positive or negative, with vegetation height.

For butterfly abundance, the best predictive model included the vegetation variables of percent cover of bare ground and percent forb cover (Table 5). In this model, total butterfly abundance was negatively associated with bare ground and was positively associated with forb cover. Neither species richness nor diversity had vegetation variables that met the criteria for entry into the model (Table 5).

3.4. *Butterfly community composition*

Butterfly community composition separated sites according to their restoration practices, especially between burned only and grazed only sites (Fig. 2). In contrast, there was little separation between grazed only and burned and grazed sites

Table 4 – Butterfly species responses to environmental variables

Butterfly species	Habitat guild	Floral	VH	LD	WS	CS	Forb	S	L	BG
Cercyonis pegala	hs		+	+**	–	+*	+	–	+	–***
Hesperia ottoe	hs			–*	+**	–*	–		–	+*
Speyeria idalia	hs	+	+	+*		+	+		+	–*
Colias eurytheme	hg	+*		+	–*	+***	+	–	+	–
Danaus plexippus	hg	+	–		–	+	+	–	+	–
Euptoieta claudia	hg	+*	–	–		–	–			+
Everes comyntas	hg	+		–	+		–	+	–	+
Megisto cymela	hg				+	+	–			–
Pieris rapae	hg			+		+	–		+	–
Strymon melinus	hg	+	–	–	+	–	–	+		+

Correlations of mean butterfly responses with environmental variables. Environmental variables listed are Floral Resources (Floral), Vegetation Height (VH), Litter Depth (LD), Percent Warm Season Grasses (WS), Percent Cool Season Grasses (CS), Percent Forb Cover (Forb), Percent Shrub (S), Percent Litter (L), and Percent Bare Ground (BG). Butterfly habitat guilds are either Habitat-specialist (hs) or Habitat-generalist (hg). Plus and minus signs indicate whether the relationship is positive or negative. Correlations with *R*-square values of <.01 are not reported. Tests were Bonferroni corrected for multiple testing within a species.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

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Table 5 – Stepwise linear regression on butterfly response variables with environmental variables measured at each site

Butterfly community response	Variables in model	+ or −	Model R^2
Abundance	Percent bare ground	−	0.49[a]
	Percent forb cover	+	
Species richness	No variables met criteria for entry		
Diversity	No variables met criteria for entry		

Variables required a significance level of <0.05 to enter into the models.
a $P < 0.05$.

(Fig. 2a). The percent variation explained by the first two axes (CCA 1 and CCA2) was 26.1%. When just the burned only and grazed only practices are examined, the CCA ordination plot of site scores shows distinct separation of the two restoration practices (Fig. 2b) and the percent variation explained by the first two axes was 36.1%.

Vegetation variables that were positively correlated with burned sites include percent cover of warm season grasses and bare ground (Fig. 2b). Vegetation components positively associated with grazed sites include percent cover of cool season grasses, forb cover, litter cover, and floral resources (Fig. 2b). Vegetation height did not show correlations with either restoration practice.

Our analyses revealed that some butterfly species were more correlated with sites from a particular restoration practice (Fig. 2c). When the locations of CCA species scores are plotted in the ordination space, the location of each species on the plot indicates its association with particular sites based on its proximity to them on the plot. Several species appear to be more strongly associated with the burned only sites including *Satyrium titus*, *H. ottoe*, *Celastrina ladon*, *Celastrina neglecta*, *Atalopedes campestris*, and *Polites mystic* (Fig. 2c). In addition, several species including *Lycaena dione*, *C. eurytheme*, *Papilio polyxenes*, *D. plexippus*, *Phyciodes tharos*, and *Polites peckius* appear to be associated with sites in the grazed only restoration practice. Most species do not appear to be more closely associated with sites in a particular restoration practice and appear clustered in the center of the plot (Fig. 2b). Habitat-specialist butterfly species were not more closely associated with sites in either restoration practice (Fig. 2d).

Discriminant analysis revealed that the abundance of a small number of butterfly species on each site can differentiate the sites into the correct restoration practice. When all three restoration practices were examined, sites were separated with 96% accuracy (1 site misclassified) using just ten species (Table 6). Looking at sites in just the burned only and grazed only practices, with five species, the misclassification rate was 0%; all sites were correctly classified (Table 7).

4. Discussion

Some researchers have found the practice of burning tallgrass prairie to be detrimental to butterfly communities. For example, Swengel (1998a) found that there were fewer habitat-specialist butterflies in burned areas than in grazed areas and that the combined effects of burning and other management practices were varied. Our analyses indicate butterfly abundance was lowest in the burned only restoration practice. However, we found that butterfly diversity was highest on these burned only sites. Similarly, researchers in a forested system of the western United States found butterfly diversity in burned sites was twice as high as in control sites (Huntzinger, 2003).

We did not find differences in the number of species that each restoration practice supported. In one study, Fleishman (2000) also reported no difference in species richness of butterflies between burned and unburned sites in central Nevada, USA. However, our finding does not suggest that the butterfly communities found at sites with different restoration practices were homogeneous; rather the CCA and discriminant analyses suggested that the composition of butterfly communities differed relative to the type of restoration practice received, especially between the burned only and grazed only restoration practices. These results are consistent with the idea that different restoration practices tend to favor some species and not others even within the same habitat guild.

Our vegetation models indicated that in terms of overall abundance, butterflies responded positively to the presence of forbs. This is not surprising since most prairie butterfly adults take nectar from a variety of native and non-native forb species. In addition, many species require forbs as their caterpillar host plants. Our models also showed that total butterfly abundance was negatively related to the percent cover of bare ground. The percent cover of bare ground was more than three times higher on burned only sites than on sites that were grazed or grazed and burned. The bare ground parameter in this model reiterated our finding that butterfly abundance was lowest in the burned only restoration practice. Because species richness and diversity did not have any parameters that met the requirements for entry into the models, we did not gain specific insights into their relationships with the vegetation variables we measured.

We found that total butterfly abundance was negatively associated with the percent cover of bare ground, however, the associations of individual species with bare ground were mixed. In a study of the western jewel butterfly (*Hypochrysops halyaetus*) on bushland sites outside of Perth, Australia, males and females within the same species responded differently to the presence of bare ground (Dover and Rowlingson, 2005). Males were positively associated with the amount of bare ground whereas females were not (Dover and Rowlingson, 2005). A high proportion of bare ground potentially increased the ability of males to find mates while sitting on perches where vegetation is sparse (Dover and Rowlingson, 2005). Increased ability to find mates in areas with a high proportion of bare ground may be a possible explanation for the positive relationship between *H. ottoe* and bare ground. Males of this species spend much of the flight period perched on *Echinacea* flowers searching for mates (Dana, 1991).

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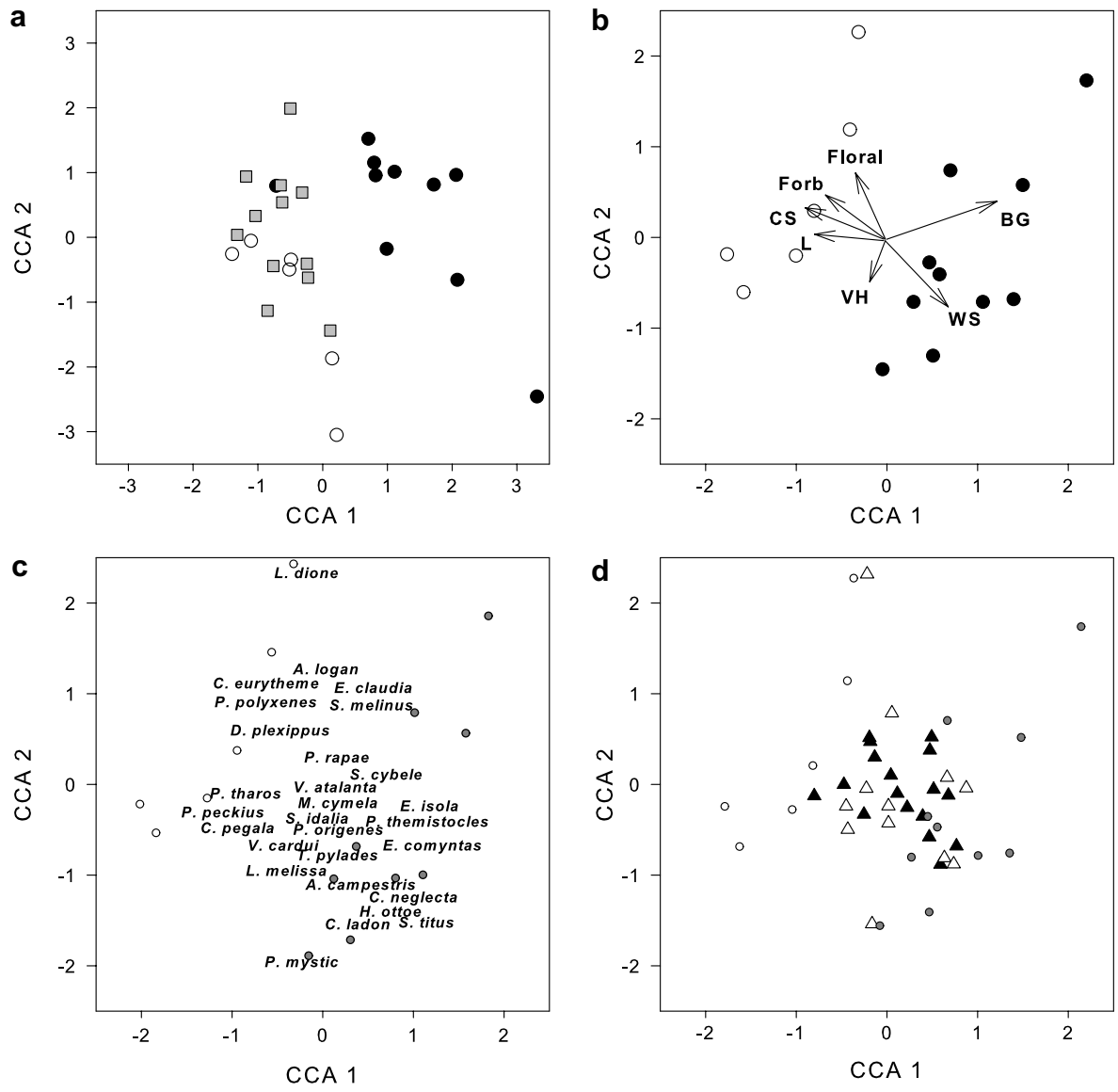

Fig. 2 – Canonical correspondence analysis ordination plots of butterfly community site scores (a, b) and butterfly species scores (c, d). (a) Locations of site scores for all three restoration practices. Burned sites are indicated with solid circles (●), grazed sites with open circles (○), and burned and grazed with shaded squares (▣). (b) Site scores for burned sites and grazed sites only. Burned sites are shown as solid circles (●) and grazed sites are shown as open circles (○). Environmental variables are indicated with arrows that represent the direction and strength (length of arrow) of their correlation with the ordination plot (loadings on each axis). Environmental variables shown are number of flowering ramets (Floral), Vegetation Height (VH), Warm Season Grasses (WS), Cool Season Grasses (CS), Forb Cover (Forb), Litter (L), and Bare Ground (BG). (c) Locations of butterfly species scores. Species names are abbreviated with the first letter of the genus and the specific epithet. Burned sites are shown as small shaded circles (◉) and grazed sites are shown as small open circles (○). (d) Locations of butterfly species scores showing habitat-specialist species as open triangles (△) and habitat-generalist species as solid triangles (▲). Burned sites are shown as small shaded circles (◉) and grazed sites are shown as small open circles (○).

Although we found no relationship between butterflies and vegetation height in our study, others have reported significant positive associations with the height and vertical density of vegetation (Reeder et al., 2005). In their study of butterflies in filter strips in Minnesota, USA, Reeder et al. (2005) found two habitat-specialist species (*S. idalia* and *C. pegala*) had positive relationships with the height and vertical density of vegetation. Although they proposed that these species may need tall vegetation to provide adequate shelter and habitat structure, we did not find this relationship in our study. The differences in our findings may be a result of differences in the variation of vegetation height between the two studies. Our study had much lower mean vegetation heights than did Reeder et al. (2005).

Previous research suggests that butterfly responses to different restoration practices can be highly variable and no one restoration practice has been found to be optimal for all species within a habitat type (Schlicht and Orwig, 1990; Swengel,

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Table 6 – Results of forward stepwise discriminant analysis on all three restoration practices (burned only, grazed only, and burned and grazed)

Order of selection	Species name	Misclassification rate (%)
1	*Danaus plexippus*	54
2	*Hesperia ottoe*	29
3	*Speyeria cybele*	21
4	*Cercyonis pegala*	18
5	*Lycaeides melissa*	14
6	*Vanessa cardui*	7
7	*Polites themistocles*	4
8	*Megisto cymela*	4
9	*Polites peckius*	7
10	*Papilio polyxenes*	4

Butterfly species with abundance of less than 10 individuals across all sites were excluded from the analysis. Butterfly species are listed in the order they were selected. Using all 10 species listed, one site was misclassified.

Table 7 – Results of forward stepwise discriminant analysis on burned only and grazed only restoration practices

Order of selection	Species name	Misclassification rate (%)
1	*Danaus plexippus*	13
2	*Echinargus isola*	13
3	*Celastrina neglecta*	6
4	*Vanessa cardui*	6
5	*Satirium titus*	0

Butterfly species with abundance of less than 10 individuals across all sites were excluded from the analysis. Butterfly species are listed in the order they were selected. Using just five species, all sites were classified correctly.

1998b). The results of our study are consistent with this finding. Within the habitat-specialist guild, individual species responses varied. Two species (*C. pegala* and *S. idalia*) were least abundant in the burned only practice while two others (*S. cybele* and *H. ottoe*) were most abundant in the burned only practice (Table 2). Because specialist species respond to management in different ways, Swengel (1998b) has advocated the use of varied management practices in order to conserve them.

One habitat-specialist and species of conservation concern in Iowa, *S. idalia*, was less abundant in the burned only restoration practice. Although rare throughout the state of Iowa, *S. idalia* was one of the most abundant species encountered in our study area. Previous studies have also found the abundance of *S. idalia* to be lower in burned sites than in sites with alternate management regimes (Swengel, 1996; Swengel, 1998b) and that moderate grazing could potentially have a positive effect on populations due to higher host plant (*Viola pedatifida*) densities on grazed sites (Debinski and Kelly, 1998). In contrast to what we found for *S. idalia*, a similar habitat-specialist species, *S. cybele*, was most abundant in the burned only restoration practice. Although these species are similar in size, coloration, and use similar host plants, *S. cybele* is able to use additional woodland host plants (*Viola* sp.) that *S. idalia* does not use. The woodlands in our study area were not burned potentially allowing *S. cybele* larvae to survive where *S. idalia* larvae could not.

Interestingly, we found another habitat-specialist species, *H. ottoe*, to have higher abundance on sites that were only burned. In one study on *H. ottoe*, Dana (1991) discovered that when fuel levels are moderate/low, fires conducted in early spring did not cause significant larval mortality and that skipper populations assessed after an early spring burn were not lower than pre-burn levels. *H. ottoe* larvae are known to build underground buried shelters where they remain through the winter into spring, potentially increasing their ability to survive during fires (Dana, 1991). However, burns conducted at other times of the year (i.e., late spring, fall) had more significant negative impacts on *H. ottoe* larvae because they were no longer protected in buried shelters (Dana, 1991). In addition to direct mortality, indirect mortality of larvae from exposure to harsh environmental conditions can occur when the litter layer is reduced after a fire (Dana, 1991).

4.1. *Conclusions and implications for management*

Because of the great diversity in butterfly species responses to different restoration practices, we do not recommend a single type of management that would benefit all species or even all species of a particular habitat guild. We found that not all habitat-specialist butterfly species were negatively affected by burning. In addition, the effects of fire on butterflies may be affected by particular aspects of a species natural history, such as over-wintering sites or location of host plants. Managers should be aware of which butterfly species are present on a particular site and which species may be negatively affected by burning prior to implementing management. Further exploration of the habitat preferences of some habitat-specialist species may be necessary to confirm our findings.

Although we found that sites managed with both fire and grazing had the highest overall abundance of butterflies, these sites did not have a higher total number of species compared with other restoration practices. Butterfly abundance was lowest on sites that were burned only, however, butterfly diversity was greatest on these sites that were managed with fire only. Our findings indicated that the butterfly communities supported by sites managed by each of the practices we examined are supporting a different suite of butterfly species. Managers seeking to maximize the number of butterfly species could achieve this goal by using multiple types of management wherever possible to provide the different microhabitat types utilized by different butterfly assemblages.

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Appendix A – Burn history and area of Loess Hills management units

Management unit	Treatment type	Unit area (ha)	Year							
			1997	1998	1999	2000	2001	2002	2003	2004
12	B	10						X		
13	B	58				X			X	X
15	B	73				X			X	
S2	B	10				X			X	
Z	B	10					X			X
R4	B	56							X	X
JC	B	102					X			
R2	B	41					X			X
R5	B	64							X	
R3	B	62							X	X
1	B&G	44					X			
2	B&G	11					X			
3–4	B&G	60					X			
5	B&G	21		X		X		X		
6	B&G	59				X				
7	B&G	20	X	X		X		X		
8	B&G	27			X					
9	B&G	64			X		X			
10	B&G	26						X	X	X
11	B&G	31						X		
B1	B&G	63							X	
B2	B&G	20							X	
KA	G	167								
KB	G	66								
KC	G	135								
L	G	158								
SA	G	84								
SB	G	43								

For burned only (B) and burned and grazed (B&G) restoration practices, an X in the column for a particular year indicates that a prescribed burn was conducted. For grazed only management units (G), no prescribed burns were conducted in the known land history and only area is indicated for these units. Study sites include Broken Kettle Grasslands Preserve, Five Ridge Prairie, and privately owned land.

Appendix B – List of all butterfly species found in study area

Species name	Common name	Guild	Burned			Grazed			Burned&Grazed			Total
			n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*
Family Papilinidae												
Papilio polyxenes	Black Swallowtail	G	0.80	4	0.20	2.00	6	0.50	0.52	3	0.13	13
Papilio cresphontes	Giant Swallowtail	W	2.00	10	0.50	1.68	5	0.42	0.68	4	0.17	19
Papilio glaucus	Tiger Swallowtail	W	7.80	39	1.95	5.32	16	1.33	4.00	24	1.00	87
Family Pieridae												
Colias eurytheme	Orange Sulfur	G	19.20	96	4.80	64.00	192	16.00	45.32	272	11.33	560
Colias philodice	Clouded Sulfur	G	0.40	2	0.10	0.32	1	0.08	0.16	1	0.04	4
Phoebis sennae	Cloudless Sulfur	G	0	0	–	0.32	1	0.08	0	0	–	1
Eurema lisa	Little Yellow	G	0.20	1	0.05	0.32	1	0.08	0	0	–	2
Pieris rapae	Cabbage White	G	4.40	22	1.10	8.00	24	2.00	10.68	64	2.67	110
Pontia protodice	Checkered White	G	0.40	2	0.10	0.68	2	0.17	0.32	2	0.08	6
Family Nymphalidae												
Danaus plexippus	Monarch	G	3.60	18	0.90	9.00	27	2.25	4.68	28	1.17	73
Megisto cymela	Little Wood Satyr	G	8.60	43	2.15	11.00	33	2.75	19.00	114	4.75	190
Cercyonis pegala	Common Wood Nymph	S	38.20	191	9.55	99.68	299	24.92	83.00	498	20.75	988
Asterocampa celtis	Hackberry Emperor	W	1.20	6	0.30	0.32	1	0.08	0	0	–	7
Limenitis archippus	Viceroy	S	0.20	1	0.05	0	0	–	0.32	2	0.08	3
Limenitis arthemis	Red-spotted Purple	W	0.60	3	0.15	0	0	–	0.32	2	0.08	5
Junonia coenia	Common Buckeye	G	0.80	4	0.20	0.32	1	0.08	0.16	1	0.04	6
Vanessa atalanta	Red Admiral	G	4.00	20	1.00	2.00	6	0.50	4.00	24	1.00	50
Vanessa cardui	Painted Lady	G	1.80	9	0.45	3.32	10	0.83	4.52	27	1.13	46
Vanessa virginiensis	American Lady	G	0.20	1	0.05	0.68	2	0.17	0.16	1	0.04	4

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Appendix B – *continued*

Species name	Common name	Guild	Burned			Grazed			Burned&Grazed			Total
			n/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*/ha	*n*	Mean	*n*
Polygonia comma	Eastern Comma	W	0.20	1	0.05	0	0	–	0	0	–	1
Chlosyne gorgone	Gorgone Checkerspot	G	0.40	2	0.10	0.68	2	0.17	0.32	2	0.08	6
Phyciodes tharos	Pearl Crescent	G	0.20	1	0.05	1.00	3	0.25	1.52	9	0.38	13
Boloria bellona	Meadow Fritillary	S	0.20	1	0.05	0	0	–	0	0	–	1
Speyeria aphrodite	Aphrodite Fritillary	S	0.20	1	0.05	0	0	–	0	0	–	1
Speyeria cybele	Great Spangled Fritillary	S	6.60	33	1.65	3.32	10	0.83	1.32	8	0.33	51
Speyeria idalia	Regal Fritillary [a]	S	22.00	110	5.50	50.00	150	12.50	47.84	287	11.96	547
Euptoieta claudia	Variegated Fritillary	G	19.80	99	4.95	19.68	59	4.92	8.16	49	2.04	207
Family Lycaenidae												
Satyrium titus	Coral Hairstreak	S	1.20	6	0.30	0	0	–	1.16	7	0.29	13
Callophrys gryneus	Olive Hairstreak	G	0.80	4	0.20	0	0	–	0	0	–	4
Strymon melinus	Gray Hairstreak	G	13.00	65	3.25	11.32	34	2.83	3.68	22	0.92	121
Lycaena hyllus	Bronze Copper	S	0	0	–	0	0	–	0.16	1	0.04	1
Lycaena dione	Gray Copper	S	0	0	–	0.32	1	0.08	1.84	11	0.46	12
Everes comyntas	Eastern Tailed Blue	G	12.60	63	3.15	7.68	23	1.92	8.00	48	2.00	134
Celastrina ladon	Spring Azure	G	1.80	9	0.45	0	0	–	0.52	3	0.13	12
Celastrina neglecta	Summer Azure	G	7.20	36	1.80	0	0	–	1.84	11	0.46	47
Lycaeides melissa	Melissa Blue	S	1.00	5	0.25	1.68	5	0.42	0.16	1	0.04	11
Echinargus isola	Reakirt's Blue	G	6.40	32	1.60	2.32	7	0.58	4.16	25	1.04	64
Family Hesperiidae												
Hesperia ottoe	Ottoe Skipper [a]	S	15.60	78	3.90	0.68	2	0.17	2.16	13	0.54	93
Polites peckius	Peck's Skipper	G	0.20	1	0.05	2.68	8	0.67	1.16	7	0.29	16
Polites mystic	Long Dash	S	0.20	1	0.05	0	0	–	1.16	7	0.29	8
Polites themistocles	Tawny-edged Skipper	G	5.00	25	1.25	3.00	9	0.75	3.00	18	0.75	52
Polites origenes	Crossline Skipper	S	1.00	5	0.25	1.84	2	0.46	0.68	11	0.17	18
Pompeius verna	Little Glassywing	W		0	–	0.32	1	0.08	0	0	–	1
Atalopedes campestris	Sachem	G	1.40	7	0.35	0.32	1	0.08	0.32	2	0.08	10
Atrytone logan	Delaware Skipper	S	1.40	7	0.35	3.32	10	0.83	1.68	11	0.42	28
Poanes hobomok	Hobomok Skipper	G	0.20	1	0.05	0	0	–	0	0	–	1
Atrytonopsis hianna	Dusted Skipper [a]	S	0.60	3	0.15	0.44	1	0.11	0.32	3	0.08	7
Lerodea eufala	Eufala Skipper	G	0	0	–	0.32	1	0.08	0.16	1	0.04	2
Thorybes pylades	Northern Cloudywing	S	1.20	6	0.30	0	0	–	1.16	7	0.29	13
Erynnis horatius	Horace's Duskywing	W	5.00	25	1.25	0	0	–	6.84	41	1.71	66
Pyrgus communis	Common-checkered Skipper	G	0.80	5	0.20	0	0	–	0.68	4	0.17	9

The total number of individuals (*n*) is summed across both years. The mean number of butterflies per unit and number of butterflies per hectare (*n*/ha) are averaged across both years. Butterflies are separated into habitat-specialist (S), habitat-generalist (G), and woodland (W) habitat guilds based on their habitat requirements for food and host plants.
a – Species of Conservation Concern Iowa DNR Draft Comprehensive Plan.

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