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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.

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-

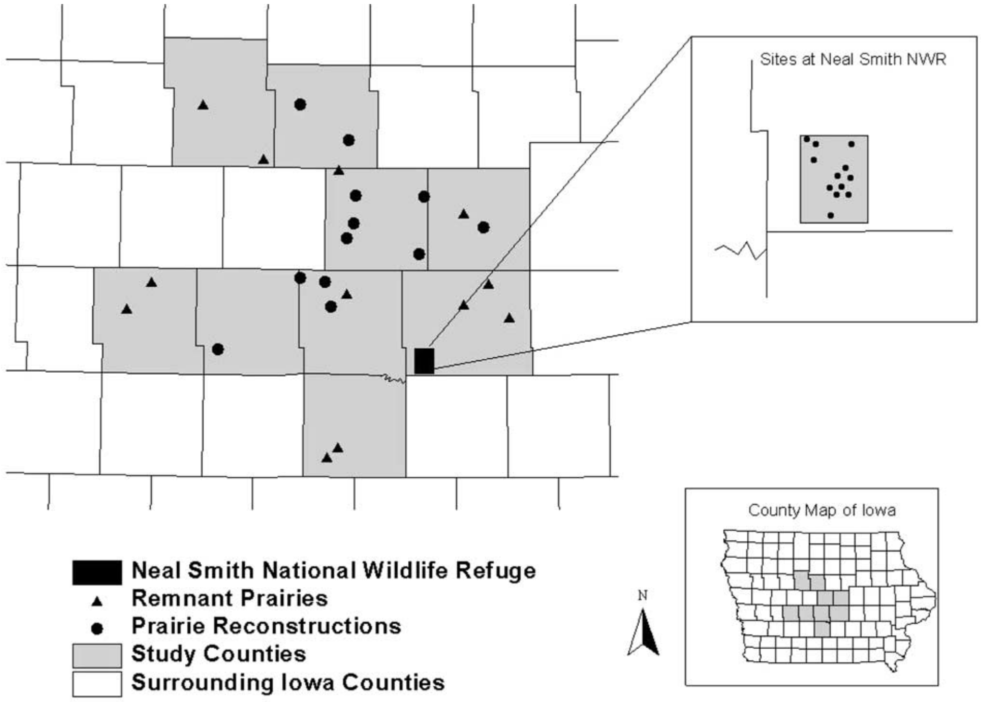

Fig. 1. Map of study areas showing approximate locations of reconstructed and remnant prairies in Central Iowa, USA. Insets show the context of the sites within Iowa and a closer view of the 12 reconstructed prairie sites at Neal Smith National Wildlife Refuge.

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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