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ORIGINAL PAPER

Comparison of butterfly communities and abundances between marginal grasslands and conservation lands in the eastern Great Plains

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Abstract The alteration and fragmentation of native tallgrass prairie in the Midwestern United States has created a need to identify other land types with the ability to support grassland butterfly species. This study examines butterfly usage of marginal grasslands, which consist of semi-natural grasslands existing within in a larger agricultural matrix, compared to grasslands managed for conservation of prairie species. Using generalized linear mixed models we analyzed how land purpose (marginal vs. conservation grasslands) affected butterfly abundance. We found grassland butterfly species to be significantly more common on conservation grasslands, whereas generalist species were significantly more common on marginal grasslands. Results of ordination analyses indicated that while many species used both types of habitats, butterfly species assemblages were distinct between habitat types and that edge to interior ratio and the floristic quality index of sites were important habitat characteristics driving this distinction. Within conservation grasslands we examined the relationship between butterfly abundance and the planting diversity used in restoring each site. We found higher diversity restorations hosted more individuals of butterflies considered habitat generalists, as well as species considered to be of conservation concern.

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Introduction

Prairie ecosystems of North America have been dramatically altered by land use changes and disruption of natural processes such as fire and grazing (Samson and Knopf 1994). These changes have been especially dramatic in the tallgrass prairie of the eastern Great Plains, where over 87 % of historic tallgrass prairie has been converted to row-crop agriculture (Samson et al. 2004). Butterflies are valued components of grassland ecosystems both for their aesthetic nature and because of the ecosystem services they provide as pollinators (New 1991). Loss and fragmentation of native habitats, along with other disturbances associated with intensive agriculture can have dramatic effects on butterfly communities (Öckinger and Smith 2007) and many populations of butterflies depending on grasslands are in decline (Swengel et al. 2011). The close link between butterflies and their natural environment make them good candidates for use as ecological indicators (Gilbert and Singer 1975; Kremen 1992; Arenz and Joern 1996). In addition, the habitat requirements and life histories of most butterfly species are well known, allowing for easier interpretation of population characteristics (Kremen 1992; Stoner and Joern 2004).

While few large blocks of native tallgrass prairie remain, many native prairie species also occur in marginal grasslands associated with agriculture. These areas include field boundaries and roadsides, as well as features such as terraces and waterways initially created to reduce soil erosion (Clark and Reeder 2007). We refer to these areas as marginal grasslands because, while these strips may have secondary benefits in conserving biodiversity and enhancing wildlife habitat (Clark and Reeder 2007), their primary purpose is unrelated to wildlife conservation. While wildlife use of marginal grasslands is receiving increased attention (Reeder et al. 2005; Davros et al. 2006; Öckinger and Smith 2007), concerns still remain about how effective such habitat strips are at maintaining native species (Whittingham 2007). Habitat fragmentation is known to have negative effects on butterfly populations (Kiviniemi and Eriksson 2002; Collinge 2000). Marginal grasslands may be unable to support breeding populations of butterflies, because they are by definition, narrow, fragmented strips (Öckinger and Smith 2007). However, even relatively small habitat patches may provide important habitat or act as corridors connecting larger patches (Panzer et al. 1995; Tscharntke et al. 2002; Dover and Settele 2009).

In this study we compare the butterfly community found on marginal grasslands to that found in grasslands managed primarily for conservation of grassland species (hereafter, conservation lands). We hypothesized that butterflies that are typically associated with grasslands (grassland or prairie specialists sensu Moranz et al. 2012) would use conservation lands more than marginal grasslands and therefore their abundance on conservation grasslands would be higher (Dover and Settele 2009; Öckinger et al. 2010). Conversely, we predicted that butterflies that are habitat generalists would use marginal grasslands to a larger extent and would have higher abundance on these lands. We also analyzed the quality of conservation lands by assessing whether forb diversity on conservation lands affects butterfly abundance. We hypothesized that higher diversity lands are more valuable to all butterflies and we expected to observe increased butterfly abundance on high diversity lands. Finally, we compared butterfly community composition on conservation and marginal grasslands to determine if different types of grassland habitat host distinctly different butterfly communities, and if so, what habitat characteristics may influence any observed differences in community composition. Our overall goal is to understand how variation in grassland habitat impacts butterfly communities in order to maximize the conservation potential of both marginal grasslands and grasslands set aside for conservation.

Methods

Study sites

Our study sites are located in eastern Nebraska and western Iowa in what was formerly the tallgrass prairie ecosystem. This region is now an agricultural landscape dominated by row crop agriculture (primarily corn and soybeans), interspersed with grasslands of various sizes and purposes (Klug et al. 2009). We used 27 grassland sites in 2004 and 51 grassland sites in 2005, located in Washington and Douglas counties of Nebraska and Harrison County of Iowa. Boundaries of each grassland site or patch were based on fence or property lines established by owners and land managers and reflect different management practices and histories.

The entire study region is human dominated and managed to some degree. We categorized each grassland patch based on its primary land-use purpose as designated by the owners or managers. Grassland patches on farms were adjacent to or embedded within row crop fields and included field margins, terraces, and waterways. Terraces and waterways are narrow strips within fields typically planted to non-native cool season grass for the primary purpose of decreasing soil erosion. Terraces and waterways tend to be actively managed to maintain high densities of grass and to eliminate weeds. Field margins that remain uncultivated, such as fencerows and ditches, divide crop fields from adjacent fields or roads. Field margins tend to be managed less intensively than terraces and waterways. In addition to linear marginal grasslands we surveyed blocks of grassland that are managed, at least in part, for conservation of the prairie community. These included both private and publicly owned conservation lands, most of which were actively managed with fire to promote a diversity of native plant species. The majority of these conservation sites were grasslands restored on former agricultural land at Desoto and Boyer Chute National Wildlife Refuges. In addition, we surveyed the University of Nebraska Omaha's restored Allwine Prairie Preserve, and a remnant of unplowed native tallgrass prairie (Cuming City Cemetery, Washington Co., NE). These conservation grasslands were divided into high, medium, and low diversity land-use categories based on planting and management histories. Low diversity sites had been planted with fewer than 35 species of grasses and forbs, including some non-native grasses, medium diversity sites were planted with between 35 and 65 species of native prairie plants, and high diversity sites were planted with greater than 65 prairie species (and most with over 100 species). Both Allwine Prairie and Cuming City Cemetery were classified as high diversity based on previous plant surveys. All of our sites fell clearly into one of these three categories based on the amount of effort and resources that had been devoted to establishing and maintaining the diversity of native forbs. Management histories provided by land managers and our measures of forb diversity supported our land-use classifications (see below). The boundaries of each grassland parcel where butterflies were sampled were digitized in ArcGIS 10.1 based on 1 m resolution aerial photographs. The area and perimeter of each grassland were calculated and used to determine the edge:interior ratio.

Butterfly surveys

We conducted butterfly surveys using a modified Pollard and Yates (1993) transect method. Surveys were conducted between 09:45 and 16:00 h when conditions were suitable for butterfly activity (limited clouds, no precipitation, sustained winds less than 15 km/h, and temperatures above 18 °C) to minimize the effect of variation in abiotic conditions on the number of butterflies detected (Pollard and Yates 1993). Butterfly censuses were conducted at least once every 2 weeks between 14 June and 15 September 2004 and 1 June and 1 September 2005. In 2004, sites were surveyed 4–6 times. In 2005, sites were surveyed 3–9 times. Survey start time was rotated among sites to decrease bias of observing species that have peak flight times during a specific time of day (New 1991). In order to compensate for a variety of patch sizes, transect lengths in 2004 corresponded to patch size, i.e. the larger the patch, the longer the transect. Previous studies have used this method and standardized butterflies per meter for habitat comparisons (Balmer and Erhardt 2000; Ouin and Burel 2002; Saarinen 2002). Sites were surveyed multiple times to account for changes in the butterfly community as the season progressed. In 2004, 170 transects were completed, totaling a distance of 111 km. After preliminary analysis of the 2004 data using species accumulation curves, we determined that fixed length transects provided equally robust estimates of the butterfly populations. In 2005 we used a fixed transect length of 250 m for all study sites. We randomly selected a 250 m transect within each patch and all butterflies within 10 m of the observer were identified. In 2005, 277 transects were completed, representing a total distance of 69 km covered. Butterflies were identified with the aid of binoculars; individuals difficult to identify were captured and then identified. Verification specimens were collected and their identities confirmed in the lab.

Vegetation measurements

We measured vegetation structure and composition in sample plots placed along butterfly transects. The marginal grasslands were long and narrow (e.g. terraces, waterways, and field margins) so vegetation survey plots were placed perpendicular to the grassland gradient to include possible differences in vegetation from the tilled field edges to the middle of the grassland strip. Width of the resulting vegetation survey plots corresponded to the width of the grassland (between 2 and 12 m). All vegetation survey plots were 1 m long. Vegetation was also measured in a subset of high and low diversity conservation grasslands. All vegetation survey plots in conservation grasslands were 1 m by 6 m. In 2004, vegetation survey plots were placed every 100 m along butterfly transects. In 2005, four vegetation survey plots were placed randomly within butterfly transects. We measured forb diversity once in 2004 (between 2 July and 9 August) and twice in 2005 (between 12 July and 24 August, with observations being at least 4 weeks apart at each site). Vegetation was measured at all marginal grassland sites but vegetation was only measured at low and high diversity conservation grassland sites and not sites categorized as medium diversity. We identified forbs to species, however, when positive identification was not possible in the field plants were recorded based on their genus or family. Within each plot we recorded number of individuals of each forb species present, and the percent cover for forbs, grasses, and bare ground. Available nectar resources were estimated based on the number of flowers in bloom in each plot (Shepherd and Debinski 2005). Forb data were used to calculate a floristic quality index (FQI) for each grassland site, representing species richness weighted towards species representative of intact tallgrass prairies (Northern Great Plains Floristic Quality Assessment Panel 2001; Taft et al. 2006). Calculation of FQI starts by applying a Coefficient of Conservatism to each forb species. Values range from 0 to 10 and represent the degree to which a plant species is tolerant of disturbance and the species' fidelity to the native vegetation of a region. Non-native plants receive a value of 0 and a plant that is indicative of the intact flora of the area and is not tolerant of disturbance would receive a $C = 10$. For our sites we used the mean of C values developed for Nebraska and Iowa. C values for Nebraska were provided by the Nebraska Natural Heritage Program (G. Steinauer, pers. comm.). C values for Iowa were downloaded from the Iowa State Herbarium in 2010 (http://www.public.iastate.edu/~herbarium/coeffici.html). FQI is then calculated based as the mean C for all forb species present at site times the square root of the number of species (Northern Great Plains Floristic Quality Assessment Panel 2001; Taft et al. 2006).

Statistical methods

All butterflies encountered were recorded. However, we excluded the non-native species *Pieres rapae* (Cabbage White) from the data analysis, as well as *Colias eurytheme* (Orange Sulphur) and *Colias philodice* (Clouded Sulphur), which were highly abundant at our sites and are commonly associated with agricultural and other disturbed landscapes. These species are very abundant within agricultural fields and we did not consider them to be targets of prairie conservation efforts. We then designated remaining native species as either habitat generalists or grassland species [i.e., grassland or prairie specialists (Moranz et al. 2012) or habitat sensitive (Davis et al. 2007)], based on published natural history information and categorizations used in other studies (Table 1). We included species described as typical of wooded or edge habitats, as well as habitat generalists, in the generalist category. Species described as relying primarily on grasslands or prairies were included in the grassland species grouping. We also included species listed as being of conservation concern by the Xerces Society Red List (2013) or by either the Iowa or Nebraska Wildlife Action Plans (Schneider et al. 2011; Iowa Department of Natural Resources 2012) within the grassland species category.

Statistical analyses were conducted using R-3.0.0 software (R Development Core Team 2013). Butterfly abundances were converted to the number of individuals per kilometer. We tested the effect of grassland category on the abundance of butterflies using generalized linear mixed models, using the glmer function from the lme4 package in R (Bates et al. 2012). Date, year, and site were treated as random effect variables whereas grassland category (marginal vs. conservation, high vs. medium vs. low planting diversity) was treated as a fixed effect. We conducted these analyses on three categories of butterfly species: habitat generalist, grassland species and those species identified as being of conservation concern. Finally, we compared abundances across habitat types for the most frequently encountered species of conservation concern, the Regal Fritillary (*Speyeria idalia*).

We used non-metric multidimensional scaling (NMDS) to analyze variation in community composition using the Bray-Curtis dissimilarity metric (Clarke 1993; Legendre and Legendre 1998). Differences in butterfly species assemblages at marginal grassland and conservation grassland sites were evaluated using a non-parametric multi-response permutation procedure (MRPP) to test for differences between groups (Zimmerman et al. 1985). The resulting index, A, ranges from 0 to 1 and describes the level of homogeneity within species groups. In a community ecology context, values above 0.1 generally indicate some level of homogeneity within groups (McCune and Grace 2002). Only sites with complete vegetation data were included in the analysis. Next, we used NMDS to evaluate which environmental factors (Table 2) could best explain differences between marginal grassland and conservation grassland sites. Marginal grasslands were smaller in area (4.4 ± 2.4 ha) than conservation grasslands (17.5 ± 5.4 ha). However, area and edge to interior ratio are highly correlated so only the latter was included in our analyses. Each environmental variable was randomly permutated for 1,000 iterations to test for significance, and goodness of fit values (R^2) were calculated. Vectors for significant environmental variables were also fit to butterfly species NMDS scores in order to assess the relationship between butterfly community diversity and relevant environmental variables. NMDS, MRPP, and environmental vector fitting was conducted using the vegan package for R (Oksanen et al. 2013).

Results

We observed a total of 5,083 individual butterflies of 42 species in 2004 and 4,364 butterflies of 42 species in 2005. There were 37 species in common between years. Five species occurred in only 2004 and another 5 occurred only in 2005; we recorded only 1–3 individuals of each species sighted in only a single year (Table 1). We excluded individuals of the three species associated with agriculture (*P. rapae, C. eurytheme* and *C. philodice*) from subsequent analyses, leaving a total of 5,441 individuals classified as either habitat generalists or grassland species. Butterflies were more abundant on marginal grasslands than on conservation grasslands (Fig. 1a). This pattern is driven by generalist butterfly species, which were more common on marginal grasslands (34.9 ± 3.3 individuals per kilometer) than on conservation grasslands (24.7 ± 3.5 individuals per kilometer, generalized linear mixed model, $df = 1$, $\chi^2 = 12.70$, $P < 0.001$, Fig. 1a). In contrast, grassland species were more common on conservation grasslands (9.8 ± 1.0 individuals per kilometer) than on marginal grasslands (2.8 ± 0.4 individuals per kilometer, generalized linear mixed model, $df = 1$, $\chi^2 = 11.07$, $P < 0.001$, Fig. 1a). Within the grassland species category, butterflies of conservation concern were more common on conservation grasslands (2.3 ± 0.3 individuals per kilometer) than on marginal grasslands (1.5 ± 0.3 individuals per kilometer) but this difference was not significant (generalized linear mixed model, $df = 1$, $\chi^2 = 0.12$, $P = 0.73$, Fig. 1b). However, the abundance of Regal Fritillaries was significantly higher on conservation grasslands (1.7 ± 0.3 individuals per kilometer) than on marginal grasslands (0.3 ± 0.1 individuals per kilometer, generalized linear mixed model, $df = 1$, $\chi^2 = 13.65$, $P < 0.001$, Fig. 1b).

Within conservation grasslands, the abundance of generalist butterfly species was significantly related to the plant diversity category of the sites (generalized linear mixed model, $df = 2$, $\chi^2 = 8.69$, $P = 0.013$). Butterfly abundance was highest on high diversity sites (31.9 ± 8.2 individuals per kilometer) and medium diversity sites (30.8 ± 7.1 individuals per kilometer) and lowest on low diversity sites (18.5 ± 3.5 individuals per kilometer, Fig. 1c). Abundance of grassland butterflies was greater on high diversity sites (13.9 ± 1.8 individuals per kilometer)

Table 1 The habitat category and number of sightings of each butterfly species at grassland sites managed primarily for conservation of native prairie species (Conserv) and marginal grassland sites associated with agriculture (Margin) in 2004 and 2005

Scientific name	Common name	2004		2005		Habitat Category	Habitat Cat. Ref.
		Conserv	Margin	Conserv	Margin		
Anatrytone logan	Delaware Skipper	4	17	19	46	Grass	1, 3, 4, 9, 12
Ancyloxypha numitor	Least Skipper	2	1	2	2	General	1, 4, 9
Atalopedes campestris	Sachem	16	6	14	1	General	7, 10, 14
Celastrina ladon	Spring Azure	5	23	1	2	General	4, 7, 10
Cercyonis pegala	Common Wood-Nymph	85	3	24	1	Grass	4, 7, 10
Chlosyne gorgone	Gorgone Checkerspot	0	0	1	1	Grass	4, 7, 8, 12
Chlosyne nycteis	Silvery Checkerspot	0	0	1	0	Grass*	3, 8, 13
Colias eurytheme	Orange Sulphur	411	1,404	758	564	Agricult	1, 3, 4, 7, 9, 12
Colias philodice	Clouded Sulphur	86	256	90	119	Agricult	1, 3, 4, 7, 9, 12
Danaus plexippus	Monarch	127	62	288	36	Grass	2, 11
Epargyreus clarus	Silver Spotted Skipper	7	19	11	17	General	4, 7, 9, 10
Erynnis baptisiae	Wild Indigo Duskywing	5	1	8	0	Grass*	6, 10, 13
Euptoieta claudia	Variegated Fritillary	6	12	19	5	General	3, 7, 10, 14
Eurema lisa	Little Yellow	17	47	19	2	General	3, 4, 14
Everes comyntas	Eastern Tailed-Blue	256	893	228	548	General	1, 3, 4, 9, 10, 12
Hemiargus isola	Reakirt's Blue	57	3	0	19	General	4, 10, 14
Junonia coenia	Common Buckeye	1	0	4	1	General	3, 4, 7, 10
Lerema accius	Clouded Skipper	1	0	1	0	General	10
Limenitis archippus	Viceroy	4	0	1	0	General	1, 3, 4, 7, 9, 10
Lim. arthemis astyanax	Red-Spotted Purple	0	1	0	1	General	1, 3, 9, 10
Lycaeides melissa	Melissa Blue	0	0	1	0	General	5, 14
Lycaena dione	Gray Copper	1	106	3	6	General	7
Lycaena hyllus	Bronze Copper	5	3	0	1	Grass*	1, 9, 13
Lycaena phlaeas	American Copper	0	0	0	1	Grass*	4, 13
Megisto cymela	Little Wood-Satyr	3	0	0	0	General	4, 7, 10
Nathalis iole	Dainty Sulphur	1	1	0	0	General	4, 10
Nymphalis antiopa	Mourning Cloak	0	1	0	0	General	4, 10
Papilio cresphontes	Giant Swallowtail	5	2	4	0	General	3, 4, 7, 10
Papilio glaucus	Eastern Tiger Swallowtail	16	9	5	4	General	3, 4, 7, 9
Papilio polyxenes	Black Swallowtail	3	6	21	5	General	1, 3, 4, 7, 9, 10, 12
Phoebis sennae	Cloudless Sulphur	10	6	2	0	General	3, 4, 10
Pholisora catullus	Common Sooty-Wing	9	53	11	40	General	1, 3, 4, 9, 10, 12
Phyciodes tharos	Pearl Crescent	34	38	13	2	General	1, 3, 4, 7, 9
Pieris rapae	Cabbage White	115	155	11	37	Agricult	1, 4, 7, 9, 12
Polites themistocles	Tawny-edged Skipper	2	0	4	1	General	1, 4, 7, 9, 10
Polygonia interrogationis	Question Mark	2	5	0	2	General	3, 4, 10
Pompeius verna	Little Glassy-wing	1	0	0	0	Grass*	10, 13
Pontia protodice	Checkered White	4	11	2	23	General	3, 4, 7, 10
Pyrgus communis	Com. Checkered Skipper	48	184	24	127	General	3, 4, 7, 10, 12
Satyrium calanus	Banded Hairstreak	3	1	1	0	Grass*	10, 13
Satyrium titus	Coral Hairstreak	0	3	0	0	Grass*	4, 13
Speyeria cybele	Great Spangled Fritillary	14	17	8	3	Grass	1, 4, 7, 9, 12
Speyeria idalia	Regal Fritillary	92	38	61	3	Grass*	6, 7, 10, 13, 15
Strymon melinus	Gray Hairstreak	0	3	2	3	General	3, 4, 7, 10
Vanessa atalanta	Red Admiral	12	61	20	28	General	1, 4, 7, 9, 10, 12
Vanessa cardui	Painted Lady	28	134	720	309	General	1, 4, 7, 9, 10

Table 1 continued

Scientific name	Common name	2004		2005		Habitat Category	Habitat Cat. Ref.
		Conserv	Margin	Conserv	Margin		
Vanessa virginiensis	American Lady	0	0	1	1	General	3, 7, 10, 12

Butterfly species considered habitat generalists and species associated with wooded or edge habitats were placed in the generalist group (General). Species considered prairie or grassland specialists were classified in the grassland group (Grass), as were species designated as being of conservation concern. Categories were based on classifications made in previously published studies. * indicates species listed as being of conservation concern nationally (Xerces Society 2013) or by the states of Iowa (Iowa Department of Natural Resources 2012) or Nebraska (Schneider et al. 2011). Three abundant species were classified as associated with agriculture (Agricult) and not included in analyses

1) Davros et al. (2006), 2) Debinski and Babbit (1997), 3) Dollar et al. (2013), 4) Evans (2008), 5) Forister et al. (2009), 6) Iowa Department of Natural Resources (2012), 7) Moranz et al. (2012), 8) Panzer et al. (1995), 9) Reeder et al. (2005), 10) Richard and Heitzman (1996), 11) Ries and Debinski (2001), 12) Ries et al. (2001), 13) Schneider et al. (2011), 14) Vogel et al. (2010), 15) Xerces Society (2013)

than on medium (11.0 ± 2.7 individuals per kilometer) or low diversity sites (6.8 ± 1.3 individuals per kilometer), however, these differences were not significant (generalized linear mixed model, $df = 2$, $\chi^2 = 2.93$, $P = 0.23$, Fig. 1c). Abundance of butterfly species listed as species of conservation concern were significantly higher on high diversity sites (3.8 ± 0.7 individuals per kilometer) than on medium (1.2 ± 0.5 individuals per kilometer) and low diversity sites (1.6 ± 0.3 individuals per kilometer, generalized linear mixed model, $df = 2$, $\chi^2 = 7.57$, $P = 0.023$, Fig. 1d). Regal Fritillaries were also most common on high diversity sites (2.9 ± 0.6 individuals per kilometer) relative to medium (0.8 ± 0.4 individuals per kilometer) and low diversity sites (1.0 ± 0.2 individuals per kilometer), but the differences were not significant (generalized linear mixed model, $df = 2$, $\chi^2 = 3.52$, $P = 0.17$, Fig. 1d).

Individuals of 30 species were observed at sites where we also collected complete vegetation data, which included 10 conservation grasslands and 13 marginal grassland sites. The MRPP analysis indicated a significant difference in butterfly community assemblages between conservation grasslands and marginal grasslands (A = 0.15, $P = 0.001$). Marginal grasslands and conservation grasslands differed in several habitat variables but only FQI and edge to interior ratio were significantly correlated to NMDS site scores (Table 2). Clustering of marginal and conservation grassland sites was evident in the plot of the NMDS sites scores, with separation of site categories occurring along a gradient parallel to axis 1 (Fig. 2). Conservation grassland sites predominately consisted of sites with high FQI values (8.81 ± 1.28) and low edge to interior ratios (0.021 ± 0.006) indicated by negative NMDS1 scores (Fig. 2), though there was substantial variation among conservation sites depending on whether they were restored and managed as high or low diversity sites (Table 3). Conversely, marginal grasslands had lower FQI values (4.37 ± 0.68) and higher edge to interior ratios (0.293 ± 0.034) and were associated with positive NMDS1 scores (Fig. 2). Edge to interior ratio was significantly, but weakly, correlated with FQI (Pearson correlation test, $R^2 = 0.21$, $df = 21$, $P = 0.02$), and was uncorrelated with any other vegetation characteristic used in the NMDS analysis (All $P > 0.20$).

Butterfly species likely to co-occur at the same sites form clusters in the plot of NMDS species scores (Fig. 3). Five of the seven grassland species (*S. calanus*, *S. idalia*, *E. baptisiae*, *D. plexippus*, and *S. cybele*) are found in close association with each other, while generalist species are more widely dispersed across the plot. Plotting the vectors for the significant habitat variables (Table 2) on the ordination plot showed the association between species clusters and the habitat variables that distinguished marginal grasslands from conservation grasslands (Fig. 3). Specifically, the species scores for all grassland species, except for *A. legan*, correlated with high FQI values and low edge to

Table 2 Habitat variables used to describe marginal grasslands and conservation grasslands

	Mean for conservation grassland sites	Mean for marginal grassland sites	NMDS1	NMDS2	R^2	*P*
Total forb abundance	433 (121)	529 (200)	−0.154	0.988	0.019	0.839
Blooms	31.6 (12.2)	29.7 (8.1)	−0.134	−0.991	0.027	0.781
Nectar species richness	2.15 (0.44)	1.57 (0.34)	−0.999	−0.054	0.059	0.538
Floristic quality index	8.81 (1.28)	4.37 (0.68)	−0.949	−0.316	0.349	0.012
Forbs (%)	15.2 (3.7)	19.7 (3.7)	−0.461	0.888	0.060	0.524
Grass (%)	73.7 (4.9)	70.6 (4.2)	−0.369	−0.930	0.022	0.790
Bare ground (%)	11.3 (2.9)	10.1 (1.9)	−0.751	−0.660	0.010	0.902
Edge to interior ratio	0.021 (0.006)	0.293 (0.034)	0.872	0.489	0.718	0.001

Mean values for all sites are given, with standard errors in parentheses. Results from the NMDS ordination are given, with values for NMDS1 and NMDS2 and their associated R^2 and *P* values

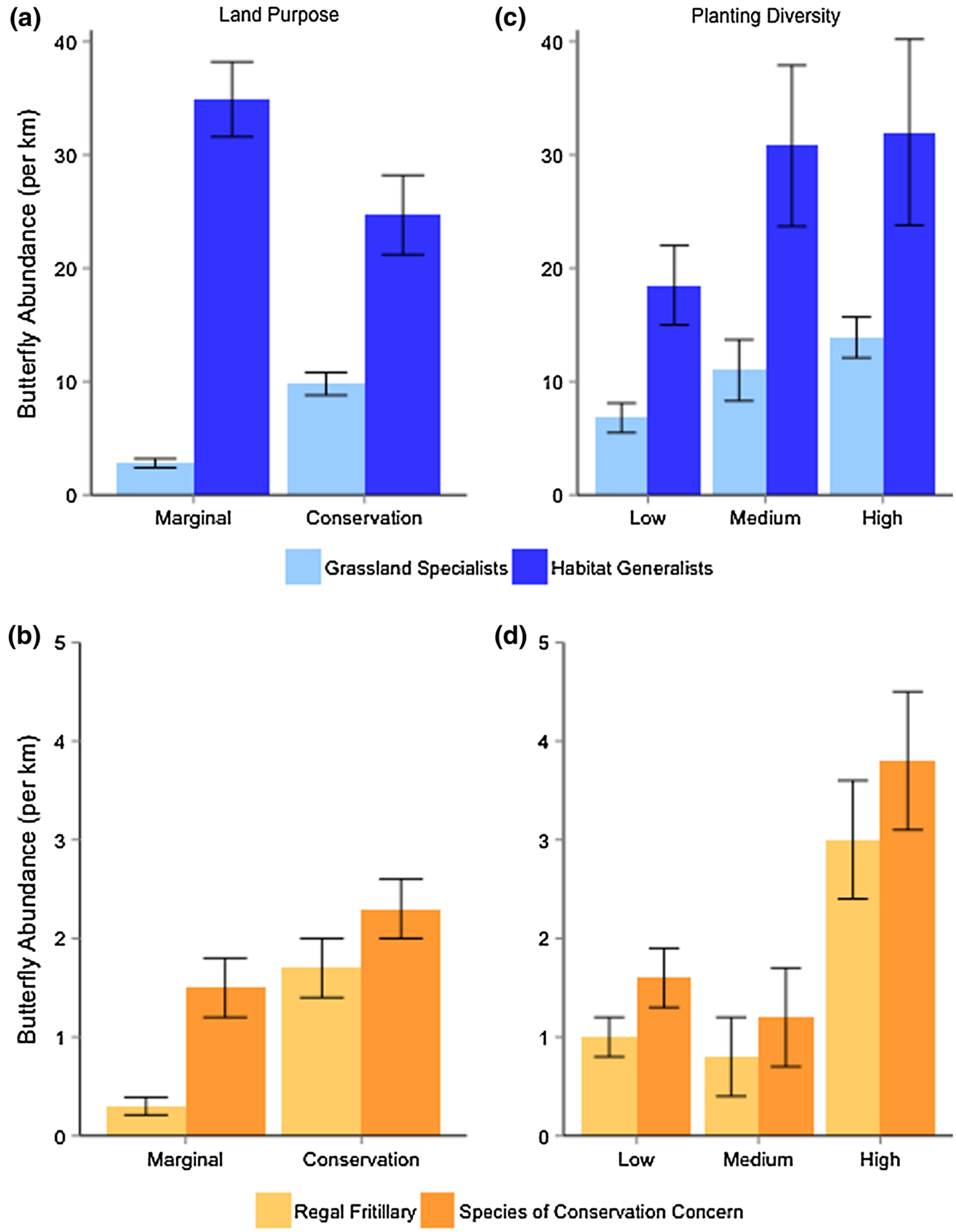

Fig. 1 Abundances of butterflies on different types of grassland sites. **a** Compares abundances of grassland butterflies and habitat generalist butterflies on marginal and conservation land. **b** Compares a subset of grassland species considered to be of conservation concern, as well as the Regal Fritillary at these same sites. **c** Compares abundances of grassland butterflies and habitat generalist butterflies on conservation grasslands restored to either low, medium, or high plant diversity, while **d** makes this comparison for species considered to be of conservation concern and the Regal Fritillary

interior ratios, the same variables considered diagnostic of conservation grasslands (Fig. 2). As a group, there was no discernible pattern of association between habitat generalist species and environmental variables (Fig. 3).

Discussion

The highest priority for conservation efforts directed towards grassland species in agriculturally dominated areas of historic tallgrass prairie has been to maintain remaining blocks of native prairie while restoring and recreating prairie on former agricultural lands. However, grassland butterfly species, including species of conservation concern such as Regal Fritillaries, are also found in marginal grasslands associated directly with agricultural fields (Ries et al. 2001; Reeder et al. 2005; Davros et al. 2006; Dollar et al. 2013). Thus, a secondary focus of conservation efforts in human-dominated landscapes could be to increase the value of marginal grasslands. This approach is analogous to the emphasis on the value of field margins in conservation programs in agricultural regions of Europe and the United Kingdom (e.g. Marshall and Moonen 2002; Marshall 2004; Woodcock et al. 2009; Haaland et al. 2011).

While we found considerable numbers of grassland butterflies on marginal grasslands, our ordination analysis

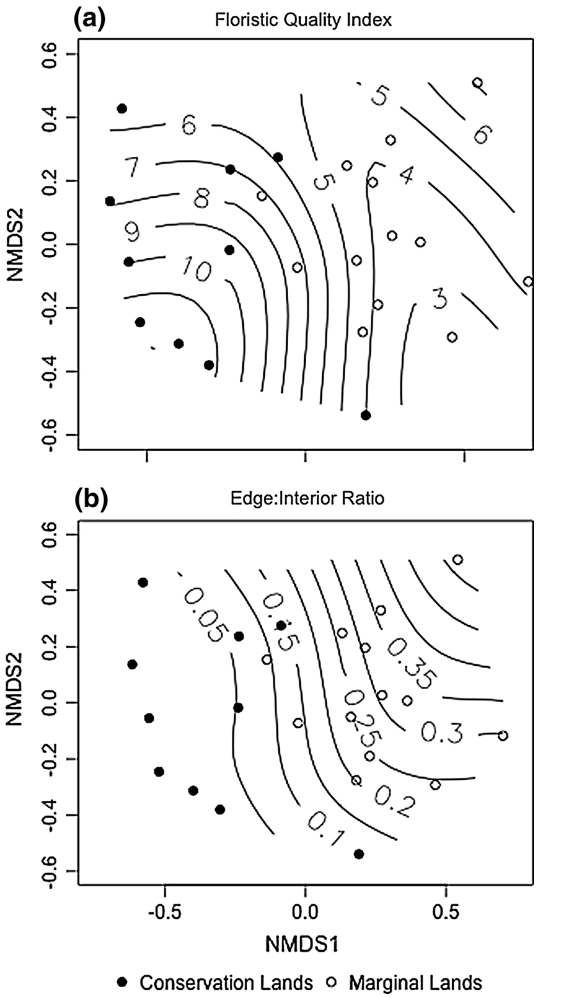

Fig. 2 Predicted values for environmental variables **a** floral quality index and **b** edge:interior ratio are overlaid onto site scores for conservation lands (*filled circles*) and marginal lands (*open circles*). We used the function ordisurf from the vegan package in R (v. 2.15.3) which utilizes a general additive model with selection done via restricted maximum likelihood (REML) to fit smoothed contours of environmental variables to the site scores

Table 3 Vegetation and site characteristics of conservation grasslands restored to low and high plant diversity

	High diversity conservation grasslands	Low diversity conservation grasslands
Total forb abundance	756 (198)	208 (105)
Blooms	85.9 (20.0)	4.0 (2.8)
Nectar species richness	3.42 (0.24)	0.96 (0.37)
Floristic quality index	12.22 (0.49)	5.53 (1.07)
Forbs (%)	30.2 (8.3)	9.5 (3.0)
Grass (%)	58.1 (10.5)	81.8 (4.3)
Bare ground (%)	11.8 (5.0)	8.9 (2.9)
Area (ha)	18.9 (4.7)	16.3 (6.1)

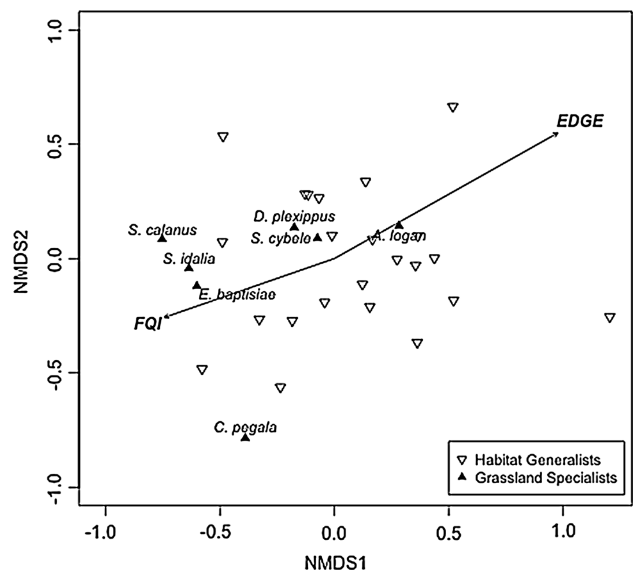

Fig. 3 NMDS ordination plot based on the Bray–Curtis distance index. Each point represents a grassland species (*filled triangle*) or habitat generalist species (*open triangle*). Overlaid are vectors (*arrows*) representing the two significant correlations between environmental variables and species compositional patterns

indicates that these sites support a distinctly different butterfly community than do sites managed specifically for conservation of grassland species (Fig. 3). We found butterfly species specializing on grassland habitat to be significantly more common on grasslands managed for conservation than on marginal grasslands (Fig. 1a). In contrast, species classified as generalists were more common on marginal grasslands than they were on conservation sites (Fig. 1a). The grassland butterfly species included several species of conservation concern (Table 1). While we found these species at marginal grasslands, they tended to be more abundant at sites managed for conservation. The Regal Fritillary, in particular, was six times more abundant on conservation lands than on marginal grassland (Fig. 1b).

Several mechanisms operating at different scales are likely driving the differences in the butterfly communities between the marginal grasslands and the conservation sites (Joern and Laws 2013). The two categories of sites differed both in the shape of the grassland patch and in vegetation characteristics (Table 2). The terraces, waterways, and road margins that comprised the marginal grasslands are linear, resulting in higher edge to interior ratios than the conservation grasslands. Edge to interior ratio contributed to the differences in butterfly assemblages observed at different sites. Among the generalist species in particular, a group of butterflies often associated with woody edges (e.g. *E. clarus, P. glaucus, V. atalanta*, and *C. ladon*) formed a cluster that was associated with sites that had a higher edge to interior ratio (Fig. 3). However, the habitat generalist category also included butterflies that are typical of disturbed open areas and were associated with sites with less edge. The sensitivity of butterfly species to the shape of grassland patches has been noted previously (Ries and Debinski 2001; Davis et al. 2007; Öckinger and Smith 2007). For example, within remnant prairie sites, Davis et al. (2007) also found significant differences in butterfly communities depending on whether sites were linear or block-shaped. This may be because grassland butterflies are more sensitive to habitat edges than are generalist species (Fleishman et al. 1999; Ries and Debinski 2001; Dover and Settele 2009; Öckinger et al. 2010). Likewise, within linear grasslands such as filter strips there is evidence that butterfly diversity and abundance increases as the width of grassland patches increases (Reeder et al. 2005; Davros et al. 2006).

The plant community also differed among the site types (Table 2). While marginal and conservation grasslands had similar densities of forbs and nectar producing blooms and had similar percent cover for grasses, forbs, and bare ground, the floristic quality index (FQI) scores contributed significantly to the separation among the sites in our ordination (Fig. 2). The FQI scores place a higher weight on species indicative of native prairie habitats and discount non-native plant species, reflecting the efforts invested in restoring and managing the grassland sites devoted to conservation. The grassland butterfly species, and especially species of conservation concern such as *S. calanus*, *S. idalia*, and *E. baptisiae*, formed an assemblage that was associated with sites with high FQI scores (Fig. 3).

Adult butterflies may respond to the abundance and diversity of nectar and larval food plants or the overall physical structure provided by the vegetation, though the strength of this relationship is variable (e.g. Sharp et al. 1974; Holl 1995; Saarinen 2002; Hawkins and Porter 2003; Waltz and Covington 2004). Decreased butterfly abundance may also be related to a reduction in forb cover (Reeder et al. 2005; Vogel et al. 2007) though we did not find a systematic difference in forb cover between marginal and conservation grasslands. Vegetation may also co-vary with grassland shape if smaller land strips contain lower plant diversity than their larger counterparts (Weibull et al. 2003). This interaction may contribute to the results of our ordination analyses because both FQI and edge to interior ratio emerged as significant variables defining differences among sites (Fig. 3). Edge to interior ratio and FQI were negatively, but weakly, correlated, ($R^2 = 0.21$) suggesting that each may contribute to the butterfly assemblages present at sites.

The fact that abundances of generalist butterflies were greater on marginal grasslands than they were on conservation grasslands (Fig. 1a) may indicate that generalist species are less dependent on native prairie plant species. It might also reflect greater habitat variability in the landscape surrounding marginal grasslands. The greater edge to interior ratio for the linear marginal grasslands means that those sites are likely to be closer to other habitat types, including woodlands, and may attract more generalist species than sites in larger grasslands managed for conservation.

The variation in habitat use by butterflies that we observed within grasslands managed for conservation lends some additional support to the importance of vegetation characteristics for butterflies. Each of our conservation sites was categorized as being low, medium or high diversity based upon the seed mixture diversity used by managers in restoring sites. Diversity of the seed mixture used in restoration is a key factor determining the diversity of the resulting grassland (Piper et al. 2007) and our high diversity conservation sites had average FQI scores of 12.22 ± 0.49 while our low diversity sites had FQI scores of 5.53 ± 1.07, similar to the scores for marginal grasslands (Tables 2 and 3). Total butterfly abundance increased with increasing restoration diversity, driven by the significantly higher numbers of individuals from generalist species at high diversity conservation sites relative to low diversity sites (Fig. 1c). This pattern indicates that butterflies are responding to the greater diversity and abundances of forbs associated with high diversity restorations (Table 3). Species of conservation concern were especially responsive to high diversity grassland restorations. As a group, these species were more abundant at high diversity sites than at either medium or low diversity restorations (Fig. 1d).

Both our study and previous work emphasize high diversity restoration of conservation lands, along with appropriate management using fire and grazing, improves the value of grasslands for butterfly communities (Collinge et al. 2003; Piper et al. 2007; Moranz et al. 2012; Myers et al. 2012). However, high quality grasslands are also difficult to create and maintain. High diversity seed mixtures are often difficult to obtain and expensive, thus limiting the area of land which can be restored (Diboll 1997; Rowe 2010). In our analysis, butterflies were no more abundant in high diversity restorations than in medium diversity grasslands (Fig. 1c). Given the cost of high diversity seed mixtures, this suggests that the creation and maintenance of medium diversity grasslands provides an attractive solution for butterfly conservation, especially if it facilitates restoration of larger areas. However, when limiting our analyses to those butterfly species considered of conservation concern (Table 1), only the high diversity restorations show a significant increase in abundances of butterflies. Indeed, while we found an average of 3.8 ($\pm$0.7) individuals per km of conservation concern at our high diversity restorations, the abundances of butterflies of conservation concern at medium (1.2 ± 0.5) and low (1.6 ± 0.3) diversity conservation sites (Fig. 1d) were similar to abundances we found at the smaller, linear marginal grasslands (1.5 ± 0.3 individuals per km; Fig. 1b).

While marginal grasslands associated with agriculture are not equivalent to lands managed specifically for conservation, these areas may still remain valuable for butterfly conservation. These linear grasslands embedded in agricultural landscapes may help connect high quality conservation lands by acting as corridors or stepping stones (Panzer et al. 1995; Tscharntke et al. 2002; Dover and Settele 2009). Haddad (1999a, b) showed that habitat restricted butterflies are more likely to use acceptable corridors in their movements, suggesting that margins could possibly function as corridors for grassland butterflies and decrease the isolation of tallgrass prairie patches. However, even small, linear grasslands have conservation value beyond their roles as corridors (Saarinen 2002; Tscharntke et al. 2002; Davis et al. 2007; Hopwood 2008). Tallgrass prairie is one of the most endangered ecosystems worldwide (Noss et al. 1995) and it is likely that this region will remain heavily dominated by row crop agriculture and with only a limited area devoted specifically to conservation purposes. One challenge will be to increase the conservation value of such marginal lands. Marginal habitats can be impacted by agricultural activities in adjacent fields, including use of herbicides, pesticides, and fertilizers, which may alter plant communities and cause direct mortality of invertebrates (Kleijn and Snoeijing 1997; Haughton et al. 2001; Roy et al. 2003; Marshall 2004; Russell and Schultz 2009; Pleasants and Oberhauser 2013). Such impacts might be reduced by providing spray buffers adjacent to important marginal habitats to minimize spray drift (Rands and Sotherton 1986). These potential impacts also suggest that marginal lands associated with lower impact agricultural practices might be given higher priority for other direct management actions to improve their conservation value for butterflies and other invertebrates (Marshall and Moonen 2002; Marshall 2004; Smith et al. 2008; Woodcock et al. 2009; Blake et al. 2011). For example, Reeder et al. (2005) suggested integrating forbs into the seed mix of filter strips to increase butterfly abundance. The positive response of grassland butterflies to the restoration of prairie vegetation along roadsides by the State of Iowa (Ries et al. 2001) demonstrates that there is the potential to increase the use by butterflies of marginal grasslands associated with agriculture. Although it will not be possible to implement such practices on all marginal grasslands, targeted investment in high priority areas has the potential to increase the conservation value of marginal grasslands.

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