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Abstract Butterflies are important components of biodiversity in grassland ecosystems and provide ecosystem services such as pollination. Although agricultural intensification has led to a scarcity of native grassland habitats within most agricultural landscapes of North America, fragmented remnants and semi-natural habitats may support diverse communities, including butterflies, as long as vital resources such as host plants are available. The United States Department of Agriculture's (USDA) Conservation Reserve Program practice CP33 Habitat Buffers for Upland Birds (USDA 2004) provides semi-natural grassland habitat in agricultural landscapes, but a knowledge gap exists about impacts of prescribed disturbance (e.g. burning or disking) on butterflies. We monitored butterfly habitat and butterfly communities on experimentally manipulated CP33 grassland buffers in Clay County, Mississippi from 2007 to 2009. Disturbance guild butterfly species richness did not differ among treatments. However, disturbance guild abundance was positively affected by disking in both the first and second growing seasons following disking, and the magnitude of this response varied between years. Effects of burning on disturbance guild abundance did not differ from the control treatment. There were no treatment differences for grassland guild butterfly abundance and species richness suggesting that periodic disturbance does not unduly impact grassland-associated butterflies in the southeastern US. Our results support current USDA practice standards that require periodic disturbance during the 10-year contract, but restrict the disturbance to 1/3 or 1/4 of grassland buffer area in a given year.

J. G. Dollar
The Xerces Society for Invertebrate Conservation, 1536 Route 9 North, Cape May Court House, NJ 08210, USA

S. K. Riffell (✉) · L. W. Burger Jr.
Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39759, USA
e-mail: sriffell@cfr.msstate.edu

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Introduction

Habitat destruction caused by conversion of natural grasslands for agriculture and human development is a major threat to butterfly populations throughout the world (New et al. 1995; Stoner and Joern 2004), including butterflies associated with grasslands of North America (Noss et al. 1995; Taron 1997). Today, ≈1 % of the original North American Tallgrass Prairie ecosystem remains (Samson and Knopf 1994; Bachand 2001). Grassland-associated butterflies have subsequently become a conservation concern (e.g. Ries et al. 2001; Davros et al. 2006; Davis et al. 2008; Vogel et al. 2010). Remaining grassland remnants are being degraded by disruption of natural disturbance regimes, woody encroachment and invasion of exotic species (Vogel et al. 2007, 2010). Butterfly communities are important components of grasslands because they contribute to biodiversity (Panzer and Schwartz 1998) and provide ecosystem services which improve and sustain human wellbeing (Daily 1997). For example, butterflies provide pollination services (Davis et al. 2008), food for other wildlife species (Doxon and Carroll 2007), ecosystem health indication (Davros et al. 2006) and wildlife viewing opportunities (Dinsmore et al. 1995). Persistence of diverse grassland butterfly communities is an important conservation concern (Schlicht and Orwig 1990; New et al. 1995; Dietrich et al. 1998; Vogel et al. 2010).

Although agricultural intensification has led to a scarcity of natural grassland habitats within agricultural landscapes, conservation programs like the Conservation Reserve Program (CRP) in the US (similar to agro-environmental schemes (AES) in Europe; e.g., Wilkinson et al. 2012) provide financial incentives to agricultural producers to establish semi-natural habitats on privately-owned cropland. The result is a substantial addition of semi-natural grasslands in agricultural landscapes that could potentially provide habitat for butterflies. In the US, the 2008 Farm Bill (Food, Conservation, and Energy Act of 2008) allocated 13 million hectares to be enrolled in CRP (USDA 2008), and over 80 % of these acres are in grass practices. These semi-natural grasslands (like many CRP habitats) may support diverse faunal communities (e.g. Weibull et al. 2003), including beneficial insects (e.g. Ockinger and Smith 2007) and butterflies (e.g. Field et al. 2005; Van Swaay et al. 2006), as long as nectar resources and host plants for butterflies are available (Davis et al. 2008).

Most natural grassland systems are maintained by periodic disturbance (fire, grazing), and semi-natural grassland habitats also need periodic disturbance to keep vegetation (and associated insect and animal communities) in early successional stages (Collins and Gibson 1990; Schultz and Crone 1998; Huntzinger 2003). Two primary options for disturbance for semi-natural grasslands in North America (like those in the CRP) are fall disking and spring burning (e.g. Greenfield et al. 2003). Burning reduces litter, inhibits woody species, facilitates growth of native grasses and opens up bare ground (Harper et al. 2007). Disking can be used as an alternative to burning in areas where burning may not be possible because it provides many of the same effects as burning (Harper et al. 2007) without the liability risk. Additionally, disking partially mimics effects of large ungulate herds which historically roamed North American grasslands by exposing soil, reducing grass dominance, and stimulating the seedbank (primarily forbs; Harper et al. 2007). Periodic disturbances are often used to maintain grassland vegetation structure to improve habitat quality for wildlife species (Harper et al. 2007) like grassland birds (Hamrick et al. 2006).

Predicting effects of burning and disking on butterflies is complicated because although some species may be negatively impacted by disturbance in the short-term, disturbance is required to maintain grasslands in a suitable successional stage for many butterfly species. Insects may also be very sensitive to environmental change, especially those that have different habitat requirements at each life stage (New et al. 1995; Samways 2007). For example, some butterflies may be affected negatively by prescribed fire because of mortality of pupae in dormant vegetation or low population sizes in small isolated remnants (Dana 1991; Swengel 1996; Panzer 2002; Samways 2007). Butterflies may also respond indirectly to effects of disturbance on host plants (Vogel et al. 2010). Disturbances which impact soil (e.g. disking) may promote more abundant and diverse forbs which can provide more abundant nectar sources (and for some species, larval host plants). A knowledge gap exists about how butterflies respond to different forms of disturbance in semi-natural grasslands, especially in the Southeastern US.

Disturbance tolerance differs among butterfly species (e.g. Swengel 1996; Harper et al. 2000; Panzer 2002). Disturbance-tolerant species (e.g. *Phoebis sennae*, Cloudless Sulfur) may be attracted to resources found on disturbed sites (e.g. annual forbs, mud puddles), whereas species with specific habitat requirements (e.g. grassland butterflies like *Nastra iherminier*, Swarthy Skipper) may be negatively affected by disturbance via mortality to overwintering life stages or dependence on perennial plant species that do not tolerate disturbance. Our objective was to evaluate effects of burning and disking of semi-natural grassland field buffers on butterflies in the southeastern US (northeast Mississippi) using a rotational scheme where <1/3 of buffers around a field were disturbed in a given year. We were particularly interested if (a) disking would facilitate a more abundant and diverse butterfly community (likely via increased nectar resources; Ekroos et al. 2010; Dollar 2011), and (b) if unmanaged control buffers would provide sufficient refugia areas for grassland (less disturbance-tolerant) butterflies so that field level diversity would be maintained. Grassland-associated butterflies (hereafter, grassland guild) might be affected negatively by burning because of damage to overwintering life stages and their comparatively low mobility to recolonize recently disturbed buffers (Swengel 1996; Vogel et al. 2010). However, we predicted that presence of refugia areas (i.e. control buffers) in the landscape would dampen effects of disturbance on grassland species by providing undisturbed source habitat nearby (Panzer 2003).

Methods

Study area

We worked at B. Bryan Farms, a privately-owned, 2,104-ha farm with row-crop and grazing operations. Located in the historical Blackland Prairie physiographic region of Northeast Mississippi, the area has a pre-settlement history of frequent fire and a post-settlement history of agricultural intensification and fire suppression (Peacock et al. 2003). Precipitation from April through August for 2007–2009 varied from year-to-year (Fig. 1). During spring of 2004, 79 crop hectares were enrolled and planted in CP33 Habitat Buffers for Upland Birds (hereafter, CP33 buffers). CP33 consists of linear strips of grassland vegetation around agricultural field borders. The initial goal of CP33 was to provide habitat for grassland birds in upland areas (Hamrick et al. 2006), but grassland buffers can benefit a variety of taxa beyond grassland birds, including insects (Marshall and Moonen 2002; Carvell et al. 2004; Haufler 2005; Davros et al. 2006; Lovell and Sullivan 2006; Olson and Wackers 2007). CP33 buffers were planted with a seed mix containing common prairie species: Big Bluestem (*Andropogon gerardii*), Little Bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), Partridge Pea (*Chamaecrista fasciculata*), Black-eyed Susan (*Rudbeckia hirta*), and Maximilian Sunflower (*Helianthus maximiliani*). The buffer plant community also included many species present in the seedbank or introduced through animal or wind dispersal. The buffers surrounded fields planted in soybean, corn, or Bermudagrass hay.

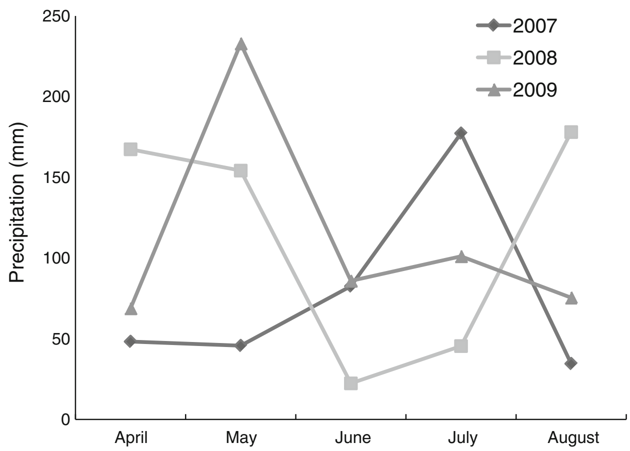

Fig. 1 Monthly precipitation (mm) for Bryan Farms, Clay County, Mississippi. Data collected at Tibbee and Aberdeen stations. April–August totals are as follows: 2007 = 388.366 mm, 2008 = 567.436 mm, 2009 = 564.134 mm

Rotational disturbance experiment

We used a rotational management plan in this study (see Fig. 2). Even though disturbance of a buffer in a particular year might negatively affect species on that particular buffer, adjacent undisturbed buffers (refugia) should allow for re-colonization of recently disked or burned buffers. Fifteen fields (containing a total of 43 buffers long enough to include a butterfly transect) were assigned randomly to one of 3 treatments (i.e. fall disk, spring burn, and no disturbance). One randomly-assigned buffer per field (one side of each field) was disturbed between growing seasons (fall disking or spring burning). In summer 2008, five buffers were disked the previous fall, 5 buffers were burned the previous spring, and 33 buffers were unmanaged (controls). In summer 2009, 5 more buffers were disked in fall 2008 and 4 more were burned in spring 2009, 24 buffers remained as controls (Fig. 2; Table 1). We distinguished between in-field controls and whole-field controls

Fig. 2 Experimental design for spring burning and fall disking treatments. Undisturbed buffers are merely outlined. Whole-field controls (*lower left of figure*) are fields which were not disturbed. In field controls are undisturbed buffers in fields with adjacent disturbed buffers

Table 1 Rotational management schedule for semi-natural buffer disturbance by year at B. Bryan Farms in Clay County, Mississippi, showing the number of buffers treated each year

	2007	2008	2009
Field control	43	11	11
Disk control		12	7
Burn control		10	6
1st growing-season post disk		5	5
1st growing-season post burn		5	4
2nd growing-seasons post disk			5
2nd growing-seasons post burn			5

in analyses. Whole-field controls were fields for which the entire perimeter buffer was neither burned nor disked during our study. In-field controls were currently undisturbed buffers in burn or disk fields attached to buffers that were disturbed during the study. Because butterflies are mobile organisms, deleterious or beneficial effects caused by disking or burning buffers could influence butterfly communities in connected buffers. In contrast, whole-field control buffers were disjunct from disturbed buffers and less likely to be influenced by butterfly population fluctuations on disturbed buffers. If undisturbed buffers effectively serve as refugia, disturbance effects on butterfly species and guilds might differ between scales of observation.

We used light disking because it promotes early-successional plant communities by cutting existing vegetation, incorporating vegetation into the soil, scarifying seed and exposing a considerable amount of bare soil (Greenfield et al. 2003). We disked in fall because fall disking normally stimulates more desirable forbs, but disking at other times of the year may stimulate less desirable agronomic weed species such as Johnsongrass (*Sorghum halepense*; Harper et al. 2007). We used prescribed burning because it maintains early-successional plant community structure, increases nutrient availability and stimulates herbaceous growth. Burning in early spring (i.e., March–April) reduces winter cover for only a short period before spring green-up and does not disrupt wildlife nesting seasons (Harper et al. 2007). Also, an early spring burn produces less smoke (which can be negatively viewed by the public) compared to a burn after spring green-up has occurred.

Butterfly counts

We used transects to sample butterflies (Pollard and Yates 1993). Three 50-m transects were placed in the center along the long axis of each buffer. Having 3 separate transects per buffer helped prevent double counting of individuals (Swengel and Swengel 1999). Along each 50-m transect, the lead author counted butterflies (including skippers) 6 times each summer (June–August 2007–2009) from 8 am to 1 pm CST (peak activity time). Transects were walked at a constant rate for 5 min, and all butterflies within 5 m of either side of transects were counted and identified to species (Ries et al. 2001). Butterflies were netted and released when necessary for identification. Due to difficulty of field identification, cogeners *Colias eurytheme* and *C. philodice* were pooled and considered one species throughout the analysis (sensu Ries et al. 2001; Reeder et al. 2005; Davros et al. 2006). Both species are common in Mississippi and have similar host-plant specificity and disturbance tolerance.

We assumed that detectability of each butterfly species was relatively constant across treatments because differences in detectability among treatments were likely to be small or lacking for several reasons. First, 6 rounds of counts each summer increased the chance of detecting all species present in the area, and visitation times for each buffer were rotated throughout summer. Second, transects were only 10-m wide at which distances the observer was unlikely to miss butterflies. Third, counts were only conducted when weather conditions were appropriate for butterfly sampling (Ries et al. 2001). Fourth, the same person collected butterfly data for all 3 years, removing variation related to multiple observers. Furthermore, methods for rigorous estimates of detectability for most butterfly communities are not currently available (Kery and Plattner 2007).

Butterfly habitat

Habitat data were collected late-July through early-August 2007–2009. Vegetation structure was characterized using a combination of 0.25-m^2 sampling plots (Ries et al. 2001) and point intercept techniques (Riffell et al. 2003) at 6 points positioned systematically along each 50-m butterfly sampling transect. Within each 0.25-m^2 sampling plot, percentage cover of grasses, native warm-season grasses, forbs and litter were estimated visually. Also, number of flowering stems, number of flowering stem types and the presence of partridge pea were recorded. In the middle of each plot, a 2-m long metal rod was placed vertically through the vegetation. We recorded height of vegetation and number of times vegetation hit each 25-cm section along the pole. Total number of hits estimated vegetation density, and number of 25-cm sections with vegetation estimated structural heterogeneity (Riffell et al. 2003). All habitat variables were averaged over the 6 sampling locations per transect and the 3 transects per buffer.

Butterfly metrics

To estimate species richness, we used cumulative richness over the 3 transects and the 6 visits for each buffer. Insofar as number of transects, transect length, and number of visits were constant across all buffers, fields, and treatments, cumulative number of species detected should provide a consistent index to richness, unaffected by sampling effort. Other butterfly metrics were totaled over the 3 transects per buffer and averaged over the 6 visits each summer. Years were analyzed separately because the rotational disturbance schedule produced a different set of treatments (i.e. time since disturbance) each year.

Butterflies were classified into one of three guilds based on previous studies (Swengel and Swengel 1999; Reeder et al. 2005; Davros et al. 2006; Vogel et al. 2007) and known plant associations (Scott 1986; Opler and Malikul 1992; Glassberg 1999; Bouseman et al. 2006). Disturbance guild species are habitat generalists and have a broad range of host- and nectar-plants (Vogel et al. 2010). Species in this guild have relatively high dispersal rates and typically have several broods per year. Grassland guild species use grasses primarily for host-plants, have lesser dispersal rates, and typically have one or two broods per year (Vogel et al. 2010). Forest guild species included species that prefer forested habitats and only secondarily use herbaceous areas. Forest guild species were included in total butterfly abundance and total species richness metrics, but other forest guild metrics were not analyzed due to low number of detections. See "Appendix" for a list of species with guild membership.

Statistical analysis: buffer and field scales

To investigate if butterflies responded differently to disturbance at different spatial scales, we separated analyses into buffer level analyses and field level analyses. In buffer level analyses, buffers were observational units; and in field level analyses, fields were observational units. If the undisturbed buffers in the rotational scheme functioned as refugia, negative effects at the buffer scale should be smaller or non-existent in the field level analysis.

For buffer level analyses, we used general linear models and SAS Proc Mixed (Littell et al. 2006) to test for effects of disturbance on butterfly abundance metrics. For richness variables that were counts, and hence Poisson distributed, we used Proc Glimmix (Littell et al. 2006). Our explanatory variable was treatment type. In 2008, the treatments were: control, disk control, disk 2007, burn control, and burn 2008. In 2009, the treatments were: control, disk control, disk 2007, disk 2008, burn control, burn 2008, and burn 2009. Our response variables for all 3 years were: abundance (of all species), abundances for guilds, individual species abundances, species richness (of all species), and species richness for guilds. We used field as a random effect. For field level analyses, we conducted similar tests, except we calculated butterfly metrics for whole fields (including both disturbed and undisturbed buffers in some fields) and used treatment (burn, disk, or control) as an explanatory variable.

We also used general linear models in SAS Proc Mixed (Littell et al. 2006) to test for effects of disturbance on the vegetation metrics. Our explanatory variable was treatment type, and levels were the same as for the butterfly analysis. Our response variables were: total grass density (number of hits on a 2.0-m pole), grass height diversity (number of sections hit), grass height, total grass cover, native warm-season grass cover, Johnsongrass cover, total forb cover, legume cover, partridge pea frequency of occurrence, litter cover, number of flowering stems, and number of flowering stem types. We used field as a random effect. Because the cost of Type II errors in management experiments is high (Benson et al. 2007), we set the a priori $\alpha = 0.10$ for all statistical tests (e.g. Riffell et al. 1996) to reduce the probability of Type II error.

Statistical analysis: pre-treatment differences

Data collected before treatments were implemented (summer 2007) allowed us to test if pre-treatment differences in butterfly and habitat variables existed among buffers, and hence might have biased our results. Pre-treatment analyses were conducted using the 2008 treatment designations in SAS Proc Mixed (Littell et al. 2006). We used $\alpha = 0.10$ and did not correct for multiple statistical tests because we wanted to account for any potential pre-treatment difference. The effects of correcting for multiple comparisons on Type II error were unacceptable in our case (e.g., Moran 2003). There were no pre-treatment (2007) differences for habitat variables except for percentage cover of native warm-season grass ($F_{2,\ 32.6} = 3.11$; $P = 0.058$; Table 2). One pre-treatment difference is close to the number of significant tests (10 % of 12 habitat variables) expected by chance alone, so it is unlikely that pre-treatment differences existed or were confounded with experimental treatments. For butterfly metrics, Delaware Skipper (*Anatrytone logan*) differed pre-treatment at the buffer ($F_{4,\ 38} = 2.33$; $P = 0.074$) and field ($F_{2,\ 11} = 5.95$; $P = 0.018$) level analyses, Little Yellow

Table 2 Least squares means (SE) for habitat variables by treatment on semi-natural grassland buffers at B. Bryan Farms, Clay County, Mississippi

Variable	Least squares means (1SE)		
	2007 (Pre-treatment)	2008	2009
Grass hits (#/0.25 m^2)			
Control	3.40 (0.30)	**2.37 (0.18) A**	2.88 (0.24)
Disk 2007	3.44 (0.50)	**1.12 (0.37) B**	1.92 (0.45)
Disk 2008			2.42 (0.45)
Burn 2008	3.84 (0.51)	**2.54 (0.37) A**	3.20 (0.45)
Burn 2009			2.86 (0.50)
	$F_{2,\ 32.2} = 0.42$; $P = 0.662$	$\mathbf{F_{2,\ 34.2} = 6.13; P = 0.005}$	$F_{4,\ 32.2} = 1.36$; $P = 0.270$
Grass section hits (#/0.25 m^2)			
Control	1.82 (0.12)	**1.86 (0.13) A**	2.18 (0.19)
Disk 2007	1.97 (0.24)	**0.90 (0.26) B**	1.53 (0.34)
Disk 2008			1.92 (0.34)
Burn 2008	1.96 (0.24)	**2.00 (0.27) A**	2.54 (0.34)
Burn 2009			2.08 (0.38)
P value	$F_{2,\ 35.3} = 0.33$; $P = 0.723$	$\mathbf{F_{2,\ 34.2} = 6.99; P = 0.003}$	$F_{4,\ 31.5} = 1.30$; $P = 0.292$
Grass height (cm)			
Control	78.44 (3.76)	**68.75 (3.84) A**	98.42 (5.89)
Disk 2007	79.29 (8.13)	**35.71 (8.29) B**	67.13 (10.85)
Disk 2008			88.61 (10.85)
Burn 2008	80.35 (8.14)	**72.90 (8.30) A**	94.25 (10.89)
Burn 2009			99.03 (12.04)
P value	$F_{2,\ 35.1} = 0.03$; $P = 0.971$	$\mathbf{F_{2,\ 35.9} = 8.03; P = 0.001}$	$F_{4,\ 32.2} = 1.98$; $P = 0.121$
Grass cover (%/0.25 m^2)			
Control	66.75 (4.44)	**43.75 (4.23) A**	41.89 (2.88)
Disk 2007	77.76 (8.95)	**16.70 (8.83) B**	39.54 (4.72)
Disk 2008			36.21 (4.72)
Burn 2008	70.36 (8.99)	**44.91 (8.85) A**	37.76 (4.78)
Burn 2009			39.04 (5.17)
P value	$F_{2,\ 34.3} = 0.82$; $P = 0.451$	$\mathbf{F_{2,\ 35.1} = 4.27; P = 0.015}$	$F_{4,\ 29.8} = 0.52$; $P = 0.723$
Native warm-season grass cover (%/0.25 m^2)			
Control	**54.82 (5.85) B**	**38.63 (4.59) A**	27.73 (2.85)
Disk 2007	**76.07 (9.68) A**	**12.67 (8.68) B**	29.86 (4.48)
Disk 2008			29.17 (4.48)
Burn 2008	**50.77 (9.81) B**	**39.46 (8.75) A**	24.79 (4.55)
Burn 2009			29.64 (4.88)
P value	$\mathbf{F_{2,\ 32.6} = 3.11; P = 0.058}$	$\mathbf{F_{2,\ 33.8} = 4.82; P = 0.014}$	$F_{4,\ 29.2} = 0.30$; $P = 0.875$
Johnsongrass cover (%/0.25 m^2)			
Control	11.47 (3.86)	4.84 (1.34)	9.92 (2.21)
Disk 2007	2.05 (7.18)	3.58 (2.13)	3.25 (3.46)
Disk 2008			3.44 (3.46)
Burn 2008	22.22 (7.24)	6.35 (2.17)	12.17 (3.52)
Burn 2009			10.35 (3.77)
P-value	$F_{2,\ 33.3} = 2.19$; $P = 0.128$	$F_{2,\ 31.7} = 0.54$; $P = 0.590$	$F_{4,\ 29.2} = 1.76$; $P = 0.164$
Forb cover (%/0.25 m^2)			
Control	25.62 (4.45)	**31.05 (3.74) B**	27.28 (3.35)

Table 2 continued

Variable	Least squares means (1SE)		
	2007 (Pre-treatment)	2008	2009
Disk 2007	21.90 (8.36)	**51.99 (8.40) A**	41.28 (6.34)
Disk 2008			25.20 (6.34)
Burn 2008	21.75 (8.42)	**35.36 (8.40) B**	26.00 (6.36)
Burn 2009			31.93 (7.06)
P value	$F_{2,\ 33.2} = 0.20$; $P = 0.821$	$\mathbf{F_{2,\ 35.9} = 2.97; P = 0.064}$	$F_{4,\ 33.2} = 1.47$; $P = 0.233$
Legume cover (%/0.25 m^2)			
Control	5.17 (1.52)	3.87 (1.31)	**2.70 (1.81) B**
Disk 2007	12.09 (3.74)	9.69 (3.38)	**15.35 (3.51) A**
Disk 2008			**4.59 (3.51) B**
Burn 2008	3.60 (3.73)	6.11 (3.38)	**0.00 (3.51) B**
Burn 2009			**1.43 (3.91) B**
P value	$F_{2,\ 37.8} = 1.71$; $P = 0.195$	$F_{2,\ 40} = 1.38$; $P = 0.264$	$\mathbf{F_{4,\ 35.1} = 3.56; P = 0.015}$
Partridge pea presence (1 = yes, 0 = no)			
Control	0.21 (0.10)	0.04 (0.03)	**0.04 (0.03) B**
Disk 2007	0.28 (0.25)	0.16 (0.07)	**0.33 (0.06) A**
Disk 2008			**0.02 (0.06) B**
Burn 2008	0.12 (0.25)	0.11 (0.07)	**0.04 (0.06) B**
Burn 2009			**0.15 (0.07) B**
P value	$F_{2,\ 40} = 0.10$; $P = 0.906$	$F_{2,\ 35.5} = 1.75$; $P = 0.188$	$\mathbf{F_{4,\ 34.9} = 5.32; P = 0.002}$
Litter cover (%/0.25 m^2)			
Control	7.43 (1.81)	**22.16 (1.51) A**	**27.23 (1.89) A**
Disk 2007	4.85 (3.29)	**17.30 (3.12) AB**	**16.46 (3.24) B**
Disk 2008			**20.35 (3.24) B**
Burn 2008	5.63 (3.32)	**10.63 (3.13) B**	**29.26 (3.27) A**
Burn 2009			**16.02 (3.57) B**
P value	$F_{2,\ 33.5} = 0.46$; $P = 0.636$	$\mathbf{F_{2,\ 34.2} = 7.25; P = 0.002}$	$\mathbf{F_{4,\ 30.5} = 5.89; P = 0.001}$
Flowering stems (#/0.25 m^2)			
Control	0.17 (0.06)	**0.04 (0.04) B**	0.22 (0.11)
Disk 2007	0.36 (0.15)	**0.16 (0.08) AB**	0.31 (0.23)
Disk 2008			0.12 (0.23)
Burn 2008	0.12 (0.15)	**0.20 (0.08) A**	0.00 (0.23)
Burn 2009			0.13 (0.26)
P value	$F_{2,\ 37.1} = 0.81$; $P = 0.453$	$\mathbf{F_{2,\ 34.3} = 3.32; P = 0.048}$	$F_{4,\ 35.2} = 0.34$; $P = 0.852$
Flowering types (#/0.25 m^2)			
Control	0.06 (0.02)	**0.02 (0.02) B**	0.05 (0.03)
Disk 2007	0.13 (0.04)	**0.07 (0.03) AB**	0.15 (0.06)
Disk 2008			0.05 (0.06)
Burn 2008	0.03 (0.04)	**0.10 (0.03) A**	0.00 (0.06)
Burn 2009			0.04 (0.06)
P value	$F_{2,\ 40} = 1.92$; $P = 0.160$	$\mathbf{F_{2,\ 35.4} = 2.95; P = 0.065}$	$F_{4,\ 35.2} = 0.34$; $P = 0.324$

The rotational disturbance within a field was separated into assigned treatment (e.g. disk control, disk fall 2007, and disk fall 2008). Pre-treatment (2007) estimates were obtained using 2008 treatments. Bold-face type and letters designate significant differences at $\alpha = 0.10$

(*Pyrisitia lisa*) differed pre-treatment at the buffer level ($F_{4,\ 28.4} = 5.99$; $P = 0.001$), and Variegated Fritillary (*Agraulis vanilla*) differed pre-treatment at the field level ($F_{2,\ 11} = 3.60$; $P = 0.063$). These two buffer level and two field level differences are less than the five significant tests expected by chance alone (10 % of 50 total tests on butterfly metrics), so it is unlikely that these differences represent true pre-treatment differences. Furthermore, when we used the

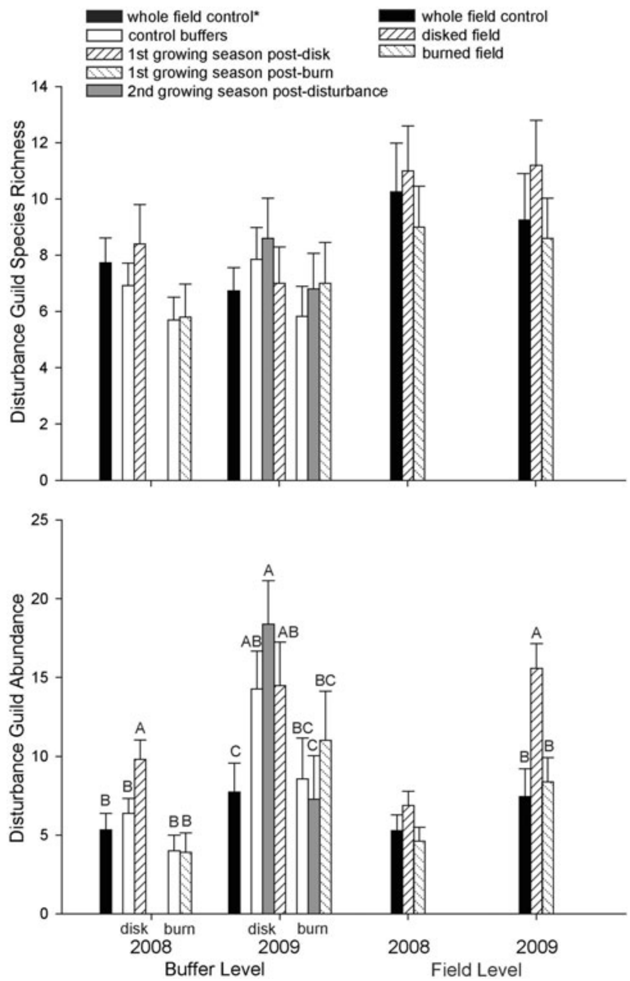

Fig. 3 Least squares means (SE) for disturbance guild species richness and abundance by year and treatment at two scales on CP33 semi-natural grassland buffers in Clay County, Mississippi. There were no significant differences within years at $\alpha = 0.10$

2007 estimates as covariates for these metrics in subsequent analyses (2008 and 2009), we reached the same conclusions (similar test statistics and *P* values) with and without pre-treatment covariates. Therefore, we assumed there were no large pre-treatment differences in habitat variables and butterfly variables and did not include covariates in subsequent analyses.

Results

Butterfly counts

We observed 7,766 individuals of 45 butterfly species during summers 2007–2009. The disturbance guild included 6,633 individuals from 18 species, comprising 85 % of total observations. The grassland guild included 907 individuals from 14 species, comprising 12 % of total

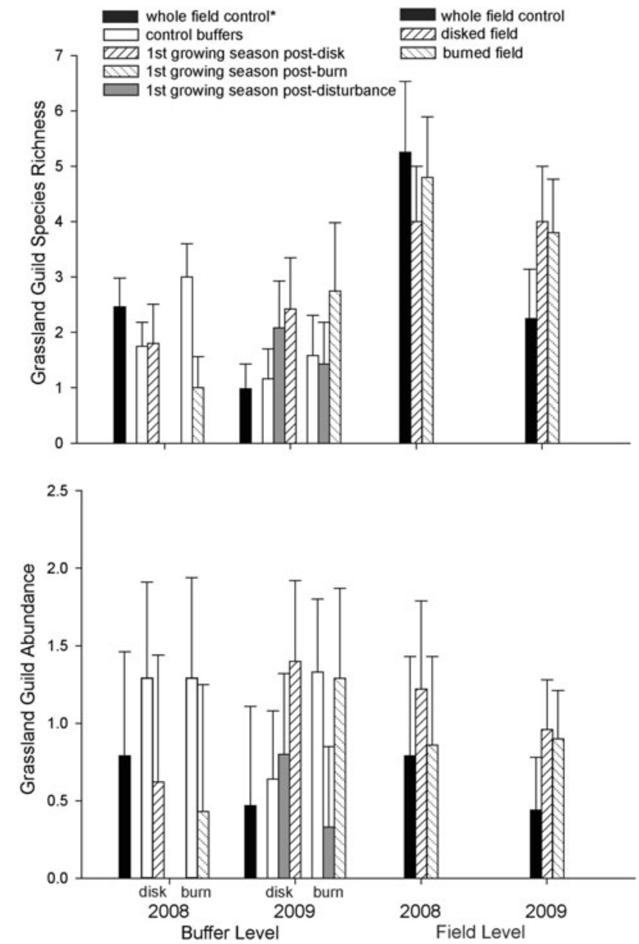

Fig. 4 Least squares means (SE) for disturbance guild species richness and abundance by year and treatment at two scales on CP33 semi-natural grassland buffers in Clay County, Mississippi. There were no significant differences within years at $\alpha = 0.10$

observations. The forest guild included 226 individuals from 13 species, comprising 3 % of total observations.

Habitat variables

During summer 2008, grass density, grass cover, grass height and native warm-season grass cover were less and forb cover was greatest on buffers disked in fall 2007 (1st growing season post-disk) compared to other treatments (Table 2). Buffers burned spring 2008 (1st growing season post-burn) did not differ from control buffers. Litter cover was greatest on control buffers, intermediate on disk 2007 buffers (1st growing season post-disk), and least on burn 2008 buffers (1st growing season post-burn; Table 2). Flowering stems and flowering types were greatest on burn 2008 buffers, intermediate on disk 2007 buffers, and least on control buffers (Table 2). Johnsongrass cover, legume cover, and partridge pea frequency of occurrence did not differ significantly between treatments in summer 2008 (Table 2).

During summer 2009, there were no treatment differences for grass density, grass cover, native warm-season grass cover, Johnsongrass cover, flowering stems, and flowering stem types (Table 2). Legume cover and partridge pea frequency of occurrence was greatest on buffers disked fall 2007 (2nd growing seasons post-disk; Table 2). Litter cover was lower on burn 2009 buffers (1st growing seasons post-burn), disk 2007 and disk 2008 compared to burn 2008 buffers (2nd growing season post-burn; Table 2).

Effects of burning and disking on butterflies

Buffer scale analyses

Total butterfly species richness did not differ among treatments during summer 2008 ($F_{4,\ 26} = 1.32$; $P = 0.290$) nor summer 2009 ($F_{6,\ 24} = 1.55$; $P = 0.206$). In 2008, overall butterfly abundance was greatest on disk 2007 buffers (1st growing season post-disk) and least on burn 2008 buffers (1st growing season post-burn; $F_{4,\ 26.5} = 2.03$; $P = 0.118$), though not with statistical significance. In 2009, overall butterfly abundance was greatest on buffers disked in 2007 (2nd growing season post-disk) and least on burn 2008 buffers (2nd growing season post-burn) and control buffers ($F_{6,\ 36} = 2.85$; $P = 0.022$).

During summer 2008 and 2009, disturbance guild species richness did not differ among treatments ($F_{4,\ 26} = 1.41$; $P = 0.257$ and $F_{6,\ 24} = 0.63$; $P = 0.704$, respectively; Fig. 3). Disturbance guild abundance was greatest on disk 2007 buffers (1st growing season post-disk in 2008 and 2nd growing season post-disk in 2009) and least on burn 2008 buffers (1st growing season post-burn and 2nd growing season post-burn in 2009; Fig. 3; $F_{4,\ 24.2} = 3.74$; $P = 0.017$ and $F_{6,\ 29.8} = 2.66$; $P = 0.034$, respectively). Furthermore, disturbance guild abundance in the disk 2008 buffers (1st growing season post-disk) did not differ from the in-field disk control buffers, and abundance on burn 2009 buffers (1st growing season post-burn) was greater than in burn control, burn 2008 (2nd growing season post-burn), and whole field control buffers.

Grassland guild species richness was greatest on whole field control and burn control buffers, intermediate on disk 2007 (1st growing season post-disk) and disk control buffers, and least on burn 2008 buffers (1st growing season post-burn) during summer 2008 ($F_{4,\ 26} = 1.94$; $P = 0.134$; Fig. 4), though not with statistical significance. There were no treatment differences for grassland guild species richness in 2009, but recently disked (disk 2008) and recently burned (burn 2009) buffers had the greatest estimates ($F_{6,\ 24} = 1.28$; $P = 0.303$; Fig. 4). There also were no treatment differences for grassland guild abundance in 2008 nor 2009 ($F_{4,\ 27.5} = 0.41$; $P = 0.801$ and $F_{6,\ 36} = 0.85$; $P = 0.538$, respectively; Fig. 4), but the abundance estimates were least on recently disked (disk 2007) and recently burned (burn 2008) buffers in 2008. In contrast, the estimates for recently disked (disk 2008) and recently burned (burn 2009) were greatest for grassland guild abundance in 2009.

Abundance of five disturbance guild species and one grassland guild species differed by treatment. During 2008, Eastern Tailed-Blue (*Cupido comyntas*) ($F_{4,\ 25.1} = 2.20$; $P = 0.098$) and Little Yellow (*P. lisa*) were most abundant on recently disked buffers (1st growing season post-disk). During 2009, Common Buckeye (*Junonia coenia*) was most abundant on disk 2007 buffers (2nd growing season post-disk) compared to other treatments ($F_{6,\ 30.4} = 2.66$; $P = 0.034$). Dun Skipper (*Euphyes vestries*) ($F_{6,\ 29.2} = 2.08$; $P = 0.087$), Hackberry Emperor (*Asterocampa celtis*) ($F_{6,\ 29.9} = 2.15$; $P = 0.077$), and Sleepy Orange (*Abaeis nicippe*) ($F_{6,\ 36} = 1.97$; $P = 0.096$) were most abundant on disk 2008 buffers (1st growing season post-disk).

Field scale analyses

There were no significant differences in overall butterfly species richness, overall abundance, disturbance guild metrics or grassland guild metrics at the field level during the first growing season (summer 2008) after the initial year of disturbance (1 buffer per field disturbed only; $F = 0.16$–1.71; $P = 0.225$–0.856). After the 2nd year of disturbance (summer 2009, when at least ½ of each field had been disturbed), total abundance ($F_{2,\ 11} = 9.77$; $P = 0.004$) was greatest for disked fields. Disturbance butterfly abundance also was greatest on disked fields ($F_{2,\ 11} = 7.74$; $P = 0.008$), but not richness ($F_{2,\ 11} = 0.93$; $P = 0.424$; Fig. 3). There were no significant differences in grassland butterfly richness and abundance ($F_{2,\ 11} = 1.12$; $P = 0.361$ and $F_{2,\ 11} = 0.75$; $P = 0.493$, respectively) during summer 2009, but both metrics were approximately 1–2 times larger on both disked and burned fields relative to fields receiving no disturbance by the 2nd growing season following disturbance (Fig. 4). American Lady (*Vanessa virginiensis*) was most abundant on disked fields in summer 2008 ($F_{2,\ 11} = 3.94$; $P = 0.051$). *Colias* spp. and Sleepy Orange (*A. nicippe*) were most abundant on disked fields in summer 2009 ($F_{2,\ 11} = 3.68$; $P = 0.060$ and $F_{2,\ 11} = 3.40$; $P = 0.071$, respectively).

Discussion

Changes in vegetation characteristics

In summer 2008, burning and disking changed buffer vegetation in some expected ways. Disking decreased grass density, grass cover, native warm-season grass cover and increased forb cover. Both burning and disking increased number of flowering stems and flowering stem types. Litter also was reduced by both disking and burning. All of these results are consistent with others investigating responses of plant communities to disking and/or burning (see Greenfield et al. 2003; Benson et al. 2007; Harper et al. 2007; Vogel et al. 2010; Dollar 2011).

Disking and burning also changed buffer vegetation in some unexpected ways. None of the responses from summer 2008 (listed above) were repeated in summer 2009 on recently treated buffers except for the decrease in litter on recently burned (burn 2009) buffers. In fact, for most variables, fall 2007 disking effects persisted into summer 2009 (2nd growing season post disturbance), but no fall 2008 disking effects were apparent in summer 2009. We are confident these results represent actual variation in disturbance effects because no pre-treatment differences existed in vegetation characteristics. These results contrast Greenfield et al. (2003) where disking effects diminished the second growing season following treatment. This suggests that in the southeastern US, other factors (e.g. weather, intensity of disking and/or burning) may have mediated vegetation responses. For example, monthly precipitation from late-spring through summer was quite different between 2008 and 2009 (Fig. 1). Higher rainfall in May 2009 compared to May 2008 could have dampened effects on buffer vegetation in 2009 by accelerating post-disturbance plant growth. Additionally, Greenfield et al.'s (2003) study focused on sod-forming species (fescue and orchardgrass) which may recover from disturbance more quickly than native bunchgrasses. Multi-year studies of vegetation will be necessary to fully describe variation in how semi-natural grasslands respond to disturbance.

Buffer level effects of disturbance on butterflies

As predicted, the two butterfly guilds responded differently to disking and burning treatments. Disking positively influenced total butterfly abundance and disturbance guild species, as we expected. However, positive effects of disking were only seen after the disk 2007 treatment. Disking in 2008 had little or no positive effect on butterfly metrics the following growing season. Because disturbance guild butterflies comprised $\approx 85\ \%$ of individuals, total butterfly abundance and species richness were driven largely by abundance and species richness of the disturbance guild. Disking of grassland areas often increases nectar-rich forbs (Jones et al. 2007) and did so in our study as well (Table 2, Dollar 2011). This likely explains why total butterfly abundance and disturbance guild abundance were related positively, as we predicted, to the 2007 disking treatment (Vogel et al. 2010). Therefore, increased nectar-rich forbs on recently disked buffers likely increased abundance of butterflies with greater dispersal ability and generalist habitat requirements (i.e., disturbance guild).

We predicted that grassland guild species would be affected negatively by disturbance at the buffer scale because of sensitivity to habitat change and their lower mobility (Swengel 1996; Vogel et al. 2010). Grassland species richness was greatest on control buffers in 2008. In 2008, abundance $>50\ \%$ lower on recently disked and burned buffers compared to control buffers, but these differences were not statistically significant. However, grassland butterfly abundance in 2009 was greatest on recently disked and recently burned buffers. This variability in responses between years may be due in part to the large temporal variability of many grassland Lepidoptertan species (e.g. Summerville et al. 2007), variability of disturbance tolerance within the grassland guild (e.g. Vogel et al. 2007) or year-to-year variability in vegetation responses to treatments (see above). Importantly, no large negative response to burning and/or disking occurred at the buffer scale for grassland butterflies. This contrasts negative effects of burning and long recovery times (approximately 70 months) of habitat-specialist butterflies on prairie remnants in Iowa (Vogel et al. 2010). Recovery times for grassland vegetation following burning may be shorter in the southeastern US compared to more northern latitudes primarily due to increased precipitation and greater solar radiation (i.e. energy and primary productivity; Harper et al. 2007). Thus, recovery times for butterfly communities on burned buffers at our study site might also be shorter compared to more northern latitudes.

Field level effects of disturbance on butterflies

We predicted that butterfly response to burning and disking would vary between the buffer level analyses and the field level analyses, especially for grassland butterflies. However, positive responses of disturbance tolerant butterflies to disking were consistent between buffer and field scale analyses. This is most likely because disking created a more diverse plant community, increased feeding opportunities for the disturbance tolerant species, and these butterfly species were able to travel the distances required to reach new nectar resources. Additionally, many disturbance guild species can overwinter in a wide range of habitat types and are not limited to grassland habitats. Therefore, any overwintering mortality from disturbance treatments would not have large negative effects on the disturbance guild compared to the grassland guild.

Grassland butterflies were not influenced by either burning or disking at the field level analyses. In fact, abundance and species richness were greater in 2009 in fields that were either disked or burned (although this was not statistically significant). Positive response to disturbance by grassland species might have been caused by a variety of factors. Control fields may have been advanced successionally in 2009 (5 years post-establishment) to a less favorable structure or species composition for butterflies. Also, the rotational management scheme results in recently disturbed buffers immediately connected to undisturbed, in-field control buffers, mimicking mosaic patterns created by historic disturbance regimes of Blackland Prairie and providing nectar resources (recently disturbed buffers) close to suitable grassland larval habitat (undisturbed buffers). Furthermore, responses at the field level (e.g. habitat mosaic) may provide more accurate descriptions of community diversity because any negative disturbance effects may be mediated by positive influences at a larger scale.

Persistence of 2007 disking effects through 2009

Effects of disking in 2007 persisted into summer 2009 (2nd growing season post-disk) for several habitat variables (i.e. percentage cover forbs, percentage cover legumes, and presence of partridge pea) and for species richness and abundance of disturbance guild butterflies. In contrast, there were little or no effects of disk 2008 treatments in summer 2009 (1st growing season post-disk). Because butterflies are tightly linked to the vegetation of their habitat, the persistent effects of disking in 2007 on vegetation (see above) most likely influenced disturbance effects on butterfly metrics in 2009. Importantly, persistent effects of disturbance of disking in 2007 were prevalent in other taxa. For example, higher density and activity of fire ants associated with disking in 2007 persisted into 2009, but disking in 2008 did not influence fire ants (Hale et al. 2011). No pre-treatment differences were found for either vegetation (Dollar 2011) or butterfly metrics (see above), so this likely represents real variation in response to disturbance. Longer term monitoring on CP33 buffers is necessary to help determine influences of year-to-year variation in wildlife and vegetation response to disturbance.

Lessons learned

The semi-natural buffers in our study supported a diverse butterfly community by providing a variety of resources crucial for each stage of development (e.g. native warm-season grasses as larval food, nectar-rich forbs for adults). These buffers were established in 2005, and we detected 45 species of butterflies during 2007–2009. Fourteen of these species (12 % of individuals detected) were grassland guild butterflies. Considering the relatively short time since establishment (5 growing seasons since establishment in spring 2005), the semi-natural grassland habitat that CP33 buffers provides may be an adequate substitute for native grassland for multiple butterfly species, and broad participation in conservation practices using native warm-season grasses and forbs may help maintain regional butterfly populations. Use of CP33 buffers by grassland species in northeast Mississippi is especially critical because only small, isolated Blackland Prairie remnants remain in the Southeast.

Our results are consistent with current USDA practice standards that require mid-contract disturbance during the 10 year life of the contract, but restrict disturbance to 1/3 or 1/4 of grassland buffers area in a given year. A rotational management regime likely promotes early-successional habitat for numerous butterflies and provides refugia areas for disturbance-sensitive species. This experiment did not use permanent, non-fire refugia (as advocated by Swengel and Swengel 2007), but the in-field controls provided sufficient refugia habitat to ensure the persistence of the grassland guild over the 2 years of the study. The rotational management also ensures habitat heterogeneity at larger spatial extents, including a diverse community of host and nectar plants for disturbance and grassland butterfly guilds. The positive relationship between butterfly abundance and forb cover reinforces the importance of including forbs species in grassland seeding mixes (Harper et al. 2007) not only for butterflies but also other beneficial insects such as bumblebees (e.g. Carvell et al. 2004).

Diversity of habitat requirements and tolerance to disturbance among butterfly species makes it difficult to recommend either disking or burning exclusively as a disturbance technique for management of conservation grasslands (i.e. mid-contract management) because one type of disturbance treatment will not benefit all species or even all species of a particular guild (Vogel et al. 2010). Disking attracted disturbance-tolerant butterflies and did not significantly decrease grassland butterflies, as well as accomplishing the management goal of maintaining a buffer plant community composed of native warm-season grasses and forbs. Moreover, disking is often easier to implement compared to burning which requires equipment, expertise, certifications, and permits that landowners typically do not have, in addition to weather restrictions on when burning can occur. Therefore, when landowners in the southeastern US must choose one type of disturbance technique for their native warm-season grass agricultural buffers (due to time and economic considerations) and butterflies are a primary objective, disking is an appropriate technique for butterfly communities. One caution is that fire might be preferred over disking in areas where fire ants are abundant because disking may increase abundance and foraging activity of fire ants (Hale et al. 2011). For landowners with resources to implement diverse disturbance techniques, a combination of disking and burning (but only on 1/3 to 1/4 of buffer area) may provide the highest conservation value. Landscape structure, habitat management, and resource availability (adult nectar and larval host plants) can be important driving forces of butterfly diversity (Weibull et al. 2000; Krauss et al. 2003; Kuussaari et al. 2007a, b), and agricultural buffers can offer multiple resources for wild plant and animal species, thereby increasing and maintaining biodiversity and enhancing ecosystem services (e.g. pollination, food chain stability) within agricultural landscapes (Kremen et al. 2007; Rands and Whitney 2010).

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Appendix

Detected butterfly species and guild classification

Disturbance Guild American Lady (*V. virginiensis*), American Snout (*Libytheana carinenta*), Black Swallowtail (*Papilio polyxenes*), Common Checkered Skipper (*Pyrgus communis*), Checkered White (*Pontia protodice*), Clouded Sulphur/Orange Sulfur (*C. philodice/C. eurytheme*), Cloudless Sulphur (*P. sennae*), Common Buckeye (*J. coenia*), Southern Dogface (*Zerene cesonia*), Eastern Tailed-Blue (*C. comyntas*), Gray Hairstreak (*Strymon melinus*), Gulf Fritillary (*Agraulis vanillae*), Little Yellow (*P. lisa*), Long-tailed Skipper (*Urbanus proteus*), Monarch (*Danaus plexippus*), Pearl Crescent (*Phyciodes tharos*), Sleepy Orange (*A. nicippe*), Variegated Fritillary (*Euptoieta claudia*).

Grassland Guild Clouded Skipper (*Lerema accius*), Crossline Skipper (*Polites origenes*), Delaware Skipper (*A. logan*), Dun Skipper (*Euphyes vestris*), Eufala Skipper (*Lerodea eufala*), Fiery Skipper (*Hylephila phyleus*), Sachem (*Atalopedes campestris*), Silver-spotted Skipper (*Epargyreus clarus*), Silvery Checkerspot (*Chlosyne nycteis*), Southern Cloudywing (*Thorybes bathyllus*), Southern Skipperling (*Copaeodes minima*), Swarthy Skipper (*Nastra lherminier*), Tawny-Edged Skipper (*Polites themistocles*), Whirlabout (*Polites vibex*).

Forest Guild Eastern Tiger Swallowtail (*Papilio glaucus*), Giant Swallowtail (*Papilio cresphontes*), Great Purple Hairstreak (*Atlides halesus*), Hackberry Emperor (*A. celtis*), Horace's Duskywing (*Erynnis horatius*), Olive/Juniper Hairstreak (*Callophrys gryneus gryneus*), Pipevine Swallowtail (*Battus philenor*), Question Mark (*Polygonia interrogationis*), Red-banded Hairstreak (*Calycopis cecrops*), Red-spotted Purple (*Limenitis arthemis*), Spicebush Swallowtail (*Papilio troilus*), Tawny Emporer (*Asterocampa clyton*), Viceroy (*Limenitis archippus*).

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