

THE INFLUENCE OF FIRE ON
LEPIDOPTERAN ABUNDANCE AND COMMUNITY STRUCTURE
IN FORESTED HABITATS OF EASTERN TEXAS

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Abstract.—Transect surveys were used to examine the influence of fire on lepidopteran communities (Papilionoidea and Hesperioidea) in forested habitats in eastern Texas. Lepidopteran abundance was greater in pine forests where prescribed fire maintained an open mid and understory compared to forests where fire had less impact on forest structure. Abundance of nectar sources paralleled this pattern of abundance. Taxonomic groups of Lepidoptera varied across forest types in patterns coincident with their dependence on nectar sources and tendency to fly in shaded habitats.

Historically, forests of the West Gulf Coastal Plain were strongly influenced by fire ignited by lightning or Native Americans (Komarek 1964; 1974; Harcombe et al. 1993; Frost 1993; 1998; Platt 1999). During the mid and late 1900s wildfires have been increasingly suppressed and replaced, to a limited extent, by prescribed fire (Frost 1993; Platt 1999). Differences in frequency, intensity and timing of prescribed fire, compared to wildfire, have resulted in a dramatic alteration of West Gulf Coastal Plain forest structure. The most obvious visible change has been the massive encroachment of woody midstory vegetation in upland forests on most of the forested landscape (Frost 1993; Platt 1999). Resulting competition has eliminated much of the diverse herbaceous community, especially in the longleaf pine savannahs that once occupied these sites (Bridges & Orzell 1989; Outcalt & Outcalt 1994).

These changes in community structure have significantly altered the forested ecosystems of the region and contributed to changes in species abundance patterns of both plants and animals. Numerous species adapted to the fire-maintained communities that existed prior to European colonization are now of conservation concern due, in part, to declining abundance as a consequence of changes in the fire regime (Conner et al. 1989; Rudolph & Burgdorf 1997).

Butterfly (Papilionoidea and Hesperioidea) communities potentially respond to changes in vegetation structure and composition resulting from differing fire regimes (Williams 1995; Mitchell & Carnes 1996;

Swengel 1996). To assess the changes in butterfly communities as a result of changes in fire regimes, this study conducted standardized surveys in a range of forested habitats in eastern Texas that have experienced different levels of impact by fire.

STUDY AREAS AND METHODS

The study was conducted on the Angelina, Davy Crockett and Sabine National Forests in eastern Texas. Forest cover on these three forests consists primarily of bottomland hardwood forests adjacent to major drainages and pine and mixed pine/hardwood forests on the uplands.

Transects were established in bottomland hardwood forest and in upland pine forests dominated by either longleaf pine (*Pinus palustris*) or loblolly (*P. taeda*) and/or shortleaf (*P. echinata*) pine. Pine-dominated forests have been managed using prescribed fire, typically in late winter or early spring. The impact on vegetation structure at specific sites has been variable due to season, intensity, and frequency of prescribed fire. Some sites, designated "burned" sites, have a history of frequent fires that have maintained an open savannah community or have had past removal of hardwood midstory vegetation by mechanical means followed by a frequent prescribed burning schedule. Mechanical midstory removal was implemented for management of the federally endangered red-cockaded woodpecker. Other sites, designated "control" sites have experienced an altered fire regime that has not been adequate to maintain the open savannah community.

Three transects were established in each of five forest types: bottomland hardwood, burned and control loblolly/shortleaf pine and burned and control longleaf pine. Surveys were conducted along a 500 m walking transect marked with flagging. Each transect was censused following the general protocols of Pollard (1977) and Gall (1985). Transects were censused once per month from March through October commencing in July 1995 and ending in June 1997. Each census consisted of two observers slowly walking the transect and recording the species of each butterfly observed. Lepidopteran classification followed Miller & Brown (1981) as modified by Scott (1986). Walking speed was adjusted to complete the transect in approximately 20 minutes. Occasionally, difficult-to-identify species were netted, identified and released. If capture for identification involved considerable time, total transect time was adjusted to allow approximately 20 minutes of actual search time. All censuses were conducted between 0900 and 1300 hrs

during periods of at least 85% sun, temperatures between 25 and 32°C, and low (<4 on the Beaufort Wind Scale) wind.

Following each individual census, nectar source abundance was estimated and recorded on an abundance scale of 1-5 ranging from absent (1) to abundant (5). This estimate was based on extensive local knowledge of the flowers visited by local butterflies obtained during three years of recording nectaring records.

After the completion of the censuses, a series of habitat measurements were conducted for each of the 15 transects. Measurements were made at the 50, 250 and 450 m points of each transect. At each point, basal area of canopy pines, canopy hardwoods, midstory pines and midstory hardwoods were determined using a 1-factor metric prism. Canopy closure was measured using a spherical densitometer. Percent cover of herbaceous and woody understory vegetation within 11.3 m of the transect points was visually estimated. Foliage density from 0-1 m in height was measured using a density board (MacArthur & MacArthur 1961).

Effects of habitat on lepidopteran census data were analyzed in 2-way ANOVAs with one missing treatment combination (bottomland, burned) using contrasts to test specific Type IV hypotheses (Milliken & Johnson 1984). This study examined the effects of fire (burned vs. control), habitat (longleaf vs. loblolly/shortleaf vs. bottomland), and the interaction between fire and habitat. A level of 0.05 was used to assess significant differences. The Shannon-Wiener Index (Pielou 1975) and the Lloyd and Ghelardi J Index (Lloyd & Ghelardi 1964) were used to quantify diversity and evenness, respectively.

RESULTS

A total of 3920 individuals of 74 species of lepidopteran were recorded during the 240 transect censuses. The species total represents approximately 70% of the regional fauna. Seasonal abundance patterns were generally similar across forest types (Figures 1-3). Peak numbers were detected in March-April, followed by a decline, and a second peak in September-October in all cases. This pattern was less evident in the control longleaf treatment. In bottomland hardwood forests and both burned and control loblolly/shortleaf forests minimum numbers were detected in the May-June period. The pattern was similar in the longleaf forests except that minimum abundance did not occur until the July-August period.

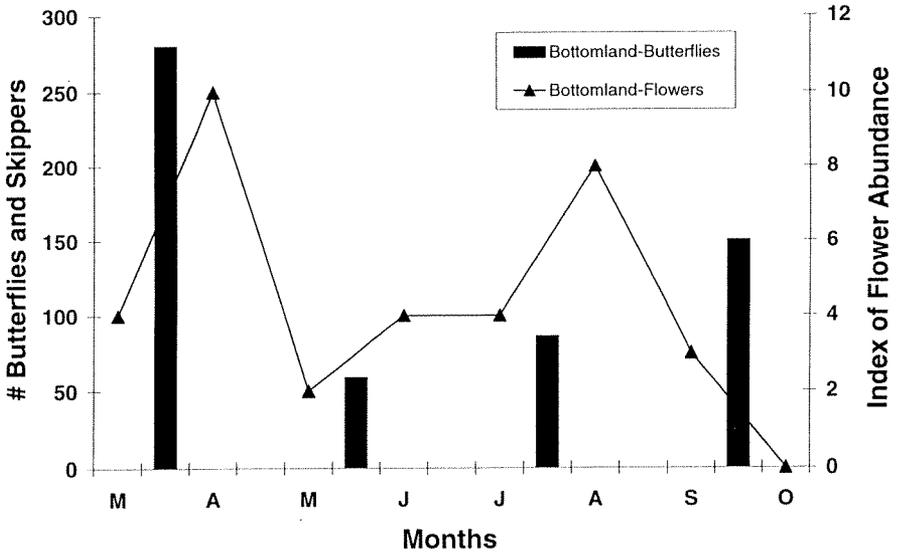


Figure 1. Butterfly and skipper abundance (bimonthly) and availability of nectar resources (monthly) in bottomland hardwood forests in eastern Texas.

Comparisons of number of species, abundance, species diversity and evenness revealed few differences among forest types (Table 1). Approximately twice the number of butterflies were detected in burned stands compared to control stands of the same forest type. Abundance in longleaf forests was approximately 50% of the levels in loblolly-shortleaf forests. Diversity and evenness measures were generally similar across treatments.

Habitat measurements were chosen to define vegetation structure (Table 2). The structure of the bottomland hardwood forests were quite different from that of the pine forests, and the habitat measures were not directly comparable due to the differing architecture of pines and angiosperms.

Results of 2-way *ANOVAs* using contrasts to test specific hypotheses are presented for both lepidopteran abundances and habitat measures in Table 3. Burned treatments had significantly more lepidopteran detections than controls and loblolly/shortleaf stands had more detections than longleaf stands.

Among the habitat variables measured, canopy basal area and percent canopy closure, did not exhibit significant differences for the hypotheses

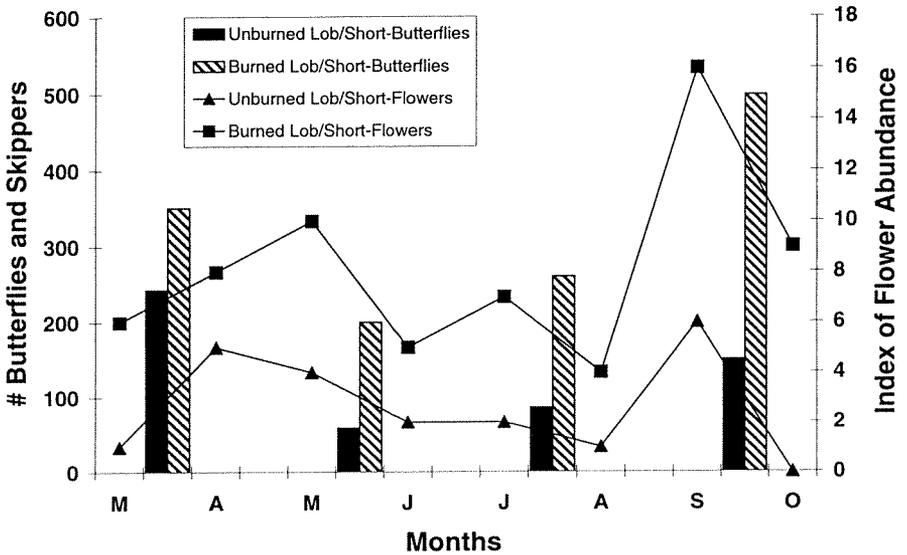


Figure 2. Butterfly and skipper abundance (bimonthly) and availability of nectar resources (monthly) in burned and control loblolly/shortleaf pine forests in eastern Texas.

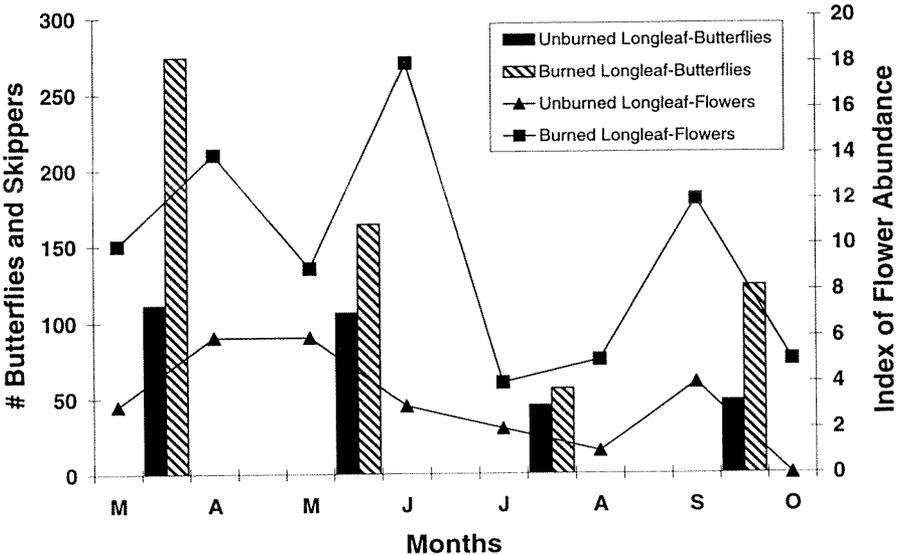


Figure 3. Butterfly and skipper abundance (bimonthly) and availability of nectar resources (monthly) in burned and control longleaf pine forests in eastern Texas.

Table 1. Mean number of species, mean number of individuals, diversity, and evenness of lepidoptera (Papilionoidea and Hesperioidea) ($n = 3$) detected by forest type during transect surveys in eastern Texas (1995-97).

Forest Type	# Species	# Individuals	Diversity	Evenness
Bottomland Hardwoods	40	373.0	2.31	0.63
Control Loblolly/Shortleaf	38	179.0	2.62	0.72
Burned Loblolly/Shortleaf	45	438.7	2.58	0.68
Control Longleaf	33	103.7	2.84	0.81
Burned Longleaf	49	208.3	2.94	0.75

tested (Table 3). The remaining habitat variables, midstory basal area, percent herbaceous cover, percent woody understory cover, and foliage density, did differ significantly between burned and control treatments. With the exception of percent woody understory, these variables also differed significantly between longleaf stands and loblolly/shortleaf stands. Only in the case of midstory basal area was there a significant interaction between fire and habitat type (longleaf vs. loblolly/shortleaf).

Within the pine dominated stands, habitat variables dependent on canopy trees (canopy tree basal area and canopy closure) did not vary significantly between burned and control treatments. The remaining habitat variables, dependent on midstory and understory vegetation, differed significantly between burned and control treatments. In both pine types, burned treatments had less woody vegetation and more herbaceous vegetation compared to the control treatments.

Nectar source abundance estimates were summed within months and forest types (Figures 1-3). The resulting indices of nectar source abundance showed peaks of abundance in spring (April-May) and late summer-fall (August-September) in all forest types (Figures 1-3). Additional peaks were also present during intervening months in the burned pine stands. In both types of pine stands, nectar indices were consistently higher in the burned treatments compared to the control treatments (Figures 1-3). The relationship of the indices of nectar source abundance to actual nectar availability is not known, however, these indices are used as a qualitative measure of resource availability in the discussions that follow.

Table 2. Habitat measurements along transects ($n = 3$) in various forest types in eastern Texas (1995-97).

Habitat Measure	Bottomland	Loblolly/Shortleaf Pine		Longleaf Pine	
	Hardwood	Control	Burned	Control	Burned
Canopy Basal Area*	10.6	16.8	15.5	15.2	17.4
Midstory Basal Area*	6.0	7.8	0.2	3.9	0.9
% Canopy Closure	97	86	85	80	77
% Herbaceous Cover	26	14	68	28	97
% Woody Understory	32	52	41	71	13
Foliage Density (m)	24.6	3.6	17.4	15.1	37.5

* Basal Area in m^2/ha .

The taxonomic composition of the butterflies detected, expressed as a percent of detections within a forest type, varied substantially across forest types (Table 4). Papilionidae and Pieridae, species that are avid nectar feeders and tend to fly in sunlight, increased in abundance with openness of the habitat and abundance of nectar resources. Representation was lowest in bottomland hardwood forest (high canopy closure values, low nectar resources) and higher in pine forest types. In burned compared to control forests, representation was greater for Papilionidae in longleaf pine forests and for Pieridae in both pine types.

Satyrinae comprised a higher percentage of the fauna in the more closed, shady habitats (bottomland hardwood forest and control pine forests) (Table 2). Representation by Satyrinae was higher in the control than burned pine forest types in both loblolly/shortleaf and longleaf pine forests. Satyrinae rarely visit nectar sources and most local species will fly in dense shade.

Species in the remaining three taxa (Lycaenidae, Nymphalidae less Satyrinae and Hesperidae) are quite variable in their dependence on nectar resources and tolerance of shady habitats. Consequently, their representation in forest faunas did not vary substantially across forest types (Table 2). There were, however, differences in species composition within these taxa across forest types. Generally, species that sought nectar resources and/or avoided shady habitats were more abundant in the burned pine forests, and species less dependent on nectar resources and more tolerant of shady habitats were more abundant in bottomland hardwood forests and control pine forests.

Table 3. Type IV hypotheses of lepidopteran abundances and habitat variables tested using contrasts.

Contrast	<i>f</i> Value	<i>P</i> Value
Lepidopteran Numbers		
Interaction between fire and habitat	1.33	0.275
Control vs. burned	7.36	0.022
Longleaf vs. loblolly/shortleaf	5.18	0.046
Canopy Basal Area		
Interaction between fire and habitat	2.49	0.146
Control vs. burned	0.20	0.665
Longleaf vs. loblolly/shortleaf	0.01	0.908
Midstory Basal Area		
Interaction between fire and habitat	7.96	0.018
Control vs. burned	18.82	0.002
Longleaf vs. loblolly/shortleaf	6.21	0.032
Percent Canopy Closure		
Interaction between fire and habitat	0.07	0.803
Control vs. burned	0.23	0.641
Longleaf vs. loblolly/shortleaf	3.03	0.113
Percent Herbaceous Cover		
Interaction between fire and habitat	1.21	0.296
Control vs. burned	88.74	0.000
Longleaf vs. loblolly/shortleaf	10.40	0.009
Percent Woody Cover		
Interaction between fire and habitat	4.45	0.061
Control vs. burned	9.64	0.011
Longleaf vs. loblolly/shortleaf	0.14	0.717
Foliage Density		
Interaction between fire and habitat	1.00	0.341
Control vs. burned	17.53	0.002
Longleaf vs. loblolly/shortleaf	13.25	0.005

DISCUSSION

Two patterns of butterfly abundance were evident in forested habitats in eastern Texas. Most obvious were abundance peaks early (April-May) and late (September) in the flight season in each forest type. The second major pattern was the increased abundance of butterflies in burned compared to control pine habitats for both pine types. These patterns are coincident with the patterns of nectar availability in these forests. In all forest types, nectar indices peak early in the season prior to complete leafout of deciduous species and again late in the season with the flowering of numerous Compositae (primarily *Eupatorium* sp., *Elephantopus* sp., *Liatrix* sp., *Bidens* sp. and *Solidago* sp.).

Table 4. Number of individuals/species (percent individuals) of selected lepidopteran taxa detected by forest type during transect surveys in eastern Texas (1995-97).

Taxon	TREATMENT				
	Bottomland Hardwood	Loblolly/Shortleaf Pine		Longleaf Pine	
		Control	Burned	Control	Burned
Papilionidae	13/4 (1)	36/4 (7)	104/6 (8)	30/4 (10)	240/6 (38)
Pieridae	7/2 (1)	53/4 (10)	434/5 (33)	13/2 (4)	63/4 (10)
Lycaenidae	138/4 (12)	55/4 (10)	187/6 (14)	26/3 (8)	22/4 (4)
Nymphalidae*	92/12 (8)	49/9 (9)	174/9 (13)	52/8 (17)	100/11 (16)
Satyrinae	642/5 (57)	272/5 (51)	149/4 (11)	127/4 (41)	84/5 (13)
Hesperioidea	227/13 (20)	72/12 (13)	268/15 (21)	63/12 (20)	116/19 (19)

* excluding Satyrinae.

Pine communities in the National Forests of eastern Texas are managed using prescribed fire on a 3-5 year interval, in part for the management of the endangered red-cockaded woodpecker, *Picoides borealis* (cf. Conner & Rudolph 1989). Wildfires are actively suppressed and have very little impact on forest vegetation due to their rarity and small size. The impact of prescribed fires on vegetation structure is dependent on a complex interaction between frequency, season, and intensity of fire, as well as differences in habitat across the landscape (Platt et al. 1988; Platt et al. 1991; Waldrop et al. 1992). Consequently, the National Forests of eastern Texas are a complex landscape of forests differentially influenced by fire. In the pine dominated forests where the above factors have resulted in vegetation structure heavily influenced by fire, midstory vegetation is sparse and the herbaceous understory is well developed. In generally similar forests where fire has not had a great impact, due in part to difference in season, intensity and frequency of fire, midstory vegetation is more dense and herbaceous vegetation in the understory is sparse.

In the pine forests of eastern Texas examined in this study, flower abundance increased with increasing change in vegetation structure due to fire. In forests where repeated fire of short return times (3-5 yrs.) had a major impact on vegetation structure (burned forests), flower abundance was greater, especially of the herbaceous species most frequently used by butterflies in these forests. In forests where fire had less impact (control forests), flower abundance was much reduced,

presumably due to the encroachment of woody vegetation in both the midstory and understory.

The pattern of nectar source availability is reflected in the abundance and species composition of butterfly communities in these forests. The well-burned forests, both loblolly/shortleaf and longleaf pine-dominated, support more individuals and a different taxonomic array than the respective unburned forests. Species that are avid nectar feeders and that do not typically fly in shady habitats are more abundant in burned forests. Species that do not commonly visit nectar sources and that do not require sunny conditions are more abundant in the control pine forests, where fire has had less impact on vegetation structure, and in bottomland hardwood forests.

The lack of significant differences in other measures of community structure (species richness, diversity, evenness) was due to low levels of habitat specialization and species replacement across habitats.

The patterns presented in this paper are for adult butterflies only, no data on the immature stages of these species was taken at these sites. These forests are a complex landscape of diverse habitats, and butterflies recorded on the various transects were not necessarily produced on those sites. However, a compilation from several sources (Opler & Malikul 1998; Scott 1986) indicates that approximately 75% of the species detected on these transects have larval stages that feed primarily on herbaceous species of plants.

Fire has been implicated in the maintenance of butterfly populations at the species (Williams 1995; Kwilosz & Knutson 1999) and community (Swengel 1996; 1998) levels. However, the impacts of fire can be both positive and negative within and across species (Panzer 1988; Swengel 1998; Dana 1991; Kwilosz & Knutson 1999). In the case of prairie-inhabiting species that are habitat specialists, fires may not be the optimum management tool in these originally fire-maintained communities (Dana 1991; Swengel 1998). However, this is, at least partly, due to breakdown of metapopulation dynamics due to extreme habitat fragmentation (Swengel 1998). Length of time intervals between successive fires and absence of population refugia may preclude re-establishment of populations of specialist species.

In the pine forests of eastern Texas the understory vegetation of well-

burned pine communities has many characteristics of well developed prairie vegetation. However, anthropogenic impacts have resulted in massive habitat alteration in this century, and remnant patches of pine savannah habitat are small and rare. No prairie or grassland specialists were detected in surveys conducted during this study. Regionally, however, several presumed specialists (Shapiro 1965; Swengel 1998) including *Problema byssus*, *Atrytonopsis hianna*, *Hesperia metea* are rare and local in remaining patches of well-burned pine savannah. Perhaps habitat alteration in eastern Texas has progressed to the extent that the specialist species are becoming regionally extinct.

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