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Research article

How does prescribed burning in grasslands of coastal southern Texas, USA, impact butterfly populations?

Rebecca R. Zerlin[a], Juan C. Elissetche[a], J. Silverio Avila-Sanchez[b], Richard J.W. Patrock[c], David B. Wester[a], Sandra Rideout-Hanzak[a,*]

[a] Caesar Kleberg Wildlife Research Institute and Department of Rangeland and Wildlife Sciences, Texas A&M University-Kingsville, 700 University Blvd., MSC 218, Kingsville, TX, 78363, USA
[b] Borderlands Research Institute, Sul Ross State University, PO Box C-21, Alpine, TX, 79832, USA
[c] Department of Biological Sciences, Texas A&M University-Kingsville, MSC 158, 700 University Boulevard, Kingsville, TX, 78363, USA

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ABSTRACT

Butterflies are important pollinators worldwide and are often sensitive indicators of ecosystem health. Prescribed fire is used in grassland to mimic historic wildfires, improve forage nutritional value, and increased forb production and diversity. However, there is little understanding of prescribed fire effects on butterfly populations. We evaluated effects of winter and summer prescribed burning and time since burning on butterfly population abundance, richness, and diversity in the Gulf Prairies and Marshes ecoregion of southern Texas. We evaluated these over a two-year period in both Gulf cordgrass and non-Gulf cordgrass grasslands. We hypothesized that summer burning would have greater positive impact on butterfly populations by increasing forb yields. We found no effects of winter burning on butterfly abundance, richness, or diversity. Summer burning reduced butterfly abundance during 5 months and richness during 6 months of our study, even as long as two years after burning. Abundance and richness were only increased by summer burning during one month of our study, in patches burned 6 and 18 months previously. Summer burning did not affect Shannon's Diversity Index; however, it did create differences in dominance among treatments as measured by Simpson's index during two months of our study. The presence of Gulf cordgrass did not affect butterfly populations; however, in Gulf cordgrass-dominated rangelands butterfly abundance was greater closer to woody mottes. We reject our hypothesis and recommend burning during winter months in southern Texas to avoid possible negative impacts on butterfly populations.

1. Introduction

Butterflies are members of the order Lepidoptera, named for their "scaly wings," which consist of two pairs of membranous wings, covered in scales. The scales may function as camouflage or as warning to predators, such as in the case of the monarch butterfly (*Danaus plexippus*). The bright orange and black coloration of monarch wings acts as a warning to potential predators about its toxicity due to cardenolides amassed from milkweed (*Asclepias* spp.) plants it eats as larvae (Davis et al., 2012). Six Lepidopteran families with 853 species have been recorded in North America (BAMONA n.d.). In Texas, US, 481 species of Lepidoptera have been documented (BAMONA n.d.).

Changes in climate and land use are altering ecosystems worldwide, and many species are forced to adapt to changes such as limited food resources, modifications to habitat, and changes in weather patterns (IPBES, 2019). Studies commonly report reductions in local Arthropod abundance because of climate change. Hallmann et al. (2017) reported declines greater than 75 % in flying insect biomass from 1989 to 2016 in Germany, and declines in biomass of beetles, moths, and caddisfly were recorded in the Netherlands across a 27-year period (Hallmann et al., 2019).

It is increasingly important to manage for butterflies because reductions in pollinator populations may impact ecosystems through a reduction in seed production, reduced pollen, or flowering plant declines (Hanberry et al., 2021). For Lepidoptera, "managing" means providing the plants necessary for all stages of the life cycle. For example, American snout (*Libytheana carienta*) caterpillars feed primarily on hackberry (*Celtis* spp.) foliage. In rangelands, specific grazing, mowing, spraying, disking, and burning methods may be useful for managing for butterflies (New et al., 1995; Feber et al., 1996) through

* Corresponding author.
E-mail address: sandra.rideout-hanzak@tamuk.edu (S. Rideout-Hanzak).

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their effects on vegetation, and this may, in turn, benefit other pollinators.

Historically, southern Texas grasslands experienced fire return intervals (FRI) as short as every 0–5 years (Stambaugh et al., 2014). Low historic FRI prevented fire-intolerant woody encroachment and reduced invasive species (Brockway et al., 2002; Britton et al., 2010). With the introduction and spread of European settlers, conventional agricultural practices and associated fire suppression, grasslands are one of the most endangered ecosystems in the world (Ceballos et al., 2010). Originally covering nearly 31 % of the United States, roughly only 60 % of grasslands remain today because of land-use changes, including lack of fire (Hays, 1994), and loss of grasslands is a potential contributor to insect population declines (Ansley and Castellano, 2006). The FRI in grasslands of southern Texas has lengthened to roughly 35 years depending on location and management preferences of the landowners (Brown and Smith, 2000). FRI studies have shown that insects respond well to burns when there is ample time between burns for recolonization (Panzer, 2002; Swengel et al., 2011). Season of burning is also an important consideration. Fire occurring during different seasons promotes different vegetation growth (Britton et al., 2010). Hansmire et al. (1988) reported that early winter (December) burns promoted higher forb yields on Texas Coastal Prairies than later winter burns (January and February).

Carbone et al. (2019) examined 65 studies across 21 countries worldwide investigating fire effects on pollinators and found mixed results depending on the arthropod order. For example, fire promoted Hymenoptera but was detrimental to Lepidoptera, especially in the case of wildfires. Swengel et al. (2011) reported mixed responses of butterflies to fire, with prairie specialists showing more negative responses to burning in four midwestern US states (Minnesota, Wisconsin, Illinois, and Iowa) over a 30-year dataset. Van Nuland et al. (2013) reported a positive response of butterflies to areas that had been burned in Tennessee, US, with higher post-fire plant visitation rates by butterflies.

There have been few studies to date of season of burning effects on butterflies (e.g., Thom et al. 205, Jue et al., 2022), and none have been conducted in Gulf cordgrass-dominated coastal grasslands of southern Texas. Our study site had an ongoing prescribed burning research project with a regime of summer and winter burning every three years or every five years; thus, we had a unique opportunity to investigate fire seasonality and time since burning effects. Our objective was to determine an optimal season of burning and FRI to manage for butterfly abundance and diversity in grasslands of the Gulf Prairies and Marshes ecoregion of southern Texas, US. We hypothesized that butterflies would have greater diversity and abundance following summer burning than winter burning because forbs can be decreased in southern Texas by late winter burning.

2. Materials and methods

2.1. Study area

Our study site was the East Foundation's El Sauz Ranch (11,330 ha, Fig. 1) in Willacy and Kenedy Counties, Texas, USA (26.5577° N, 97.4263° W). The ranch is located in the Gulf Prairies and Marshes ecoregion (Gould et al., 1960) and is bordered by the hypersaline Laguna Madre on the east. Representative graminoid species are: Gulf cordgrass (*Spartina spartinae* [Trin.] Merr. ex Hitchc.), purple dropseed (*Sporobolus purpurascens* (Sw.) Ham.), brownseed paspalum (*Paspalum plicatulum* Michx.), Hartweg's paspalum (*P. hartwegianum* Fourn.), fringed signalgrass (*Urochloa ciliatissima* (Buckley) R. Webster) and red

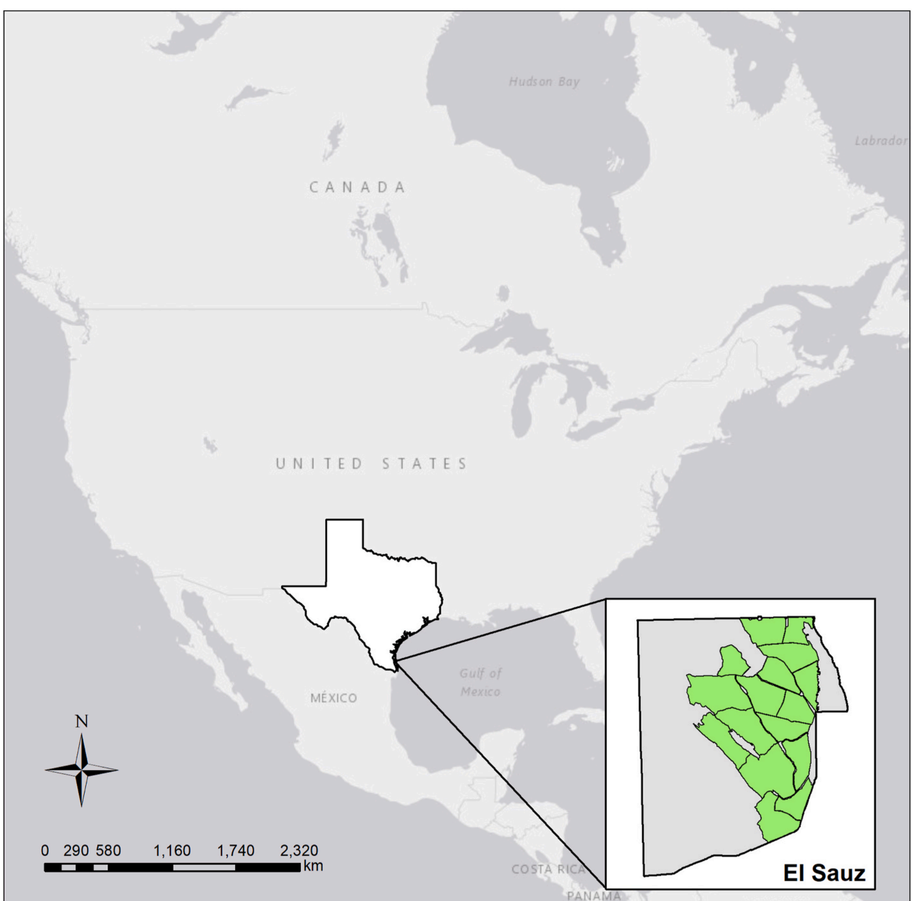

Fig. 1. General location of East Foundation's El Sauz Ranch in coastal southern Texas, USA, with treatment patches shown in green (as seen in Zerlin et al., 2023).

lovegrass (*Eragrostis secundiflora* J. Presl) (SSS n.d.).

Vegetation adjacent to the coast is predominantly Gulf cordgrass, a native bunchgrass that forms almost pure monocultures in large areas described as the Sandy Flat Cordgrass Prairie ecological site (SSS n.d.). Inland from the Gulf cordgrass is a mixed grass community dominated by seacoast bluestem (*Schizachyrium scoparium* [Michx.] Nash), Gulf-dune paspalum (*Paspalum monostachyum* Vasey), and a greater variety of other herbaceous plants than occurs in the Gulf cordgrass community. Average rainfall for the area is approximately 658 mm and a mean temperature fluctuation from 18.9 to 26.7 °C (NOAA n.d.).

Common woody species include honey mesquite (*Neltuma* (formerly *Prosopis*) *glandulosa* [Torr.] Britton & Rose), huisache (*Vachellia farnesiana* [L.] Wight & Arn.), blackbrush (*V. rigidula* [Benth.] Seigler & Ebinger), and others. These plants may grow together in groups known as mottes, small stands of trees on a prairie ranging from 0.1 to over 81 ha and consisting of as few as 2 to several thousand trees (Beasom and Haucke, 1975). Oak mottes in southern Texas consist predominantly of coastal live oak (*Quercus virginiana* Mill.) and can be found in sandy soils of the coastal plains. Often these stands have a different ground cover, largely dominated by tree leaf litter, compared to the nearby vegetation. Live oaks are the larval hosts for Horace's Duskywing (*Erynnis horatius*), White M hairstreak (*Parrhasius m-ablum*), and 'Northern' Southern hairstreak (*Satyrium favonius ontario*) (Ladybird Johnson Wildflower Center, 2022). Common soils in the study area included: Galveston fine sand (Mixed, hyperthermic Oxyaquic Udipsamments; GaB), Sauz loamy fine sand (Mixed, active, hyperthermic Typic Natraqualf; Sz), Mustang fine sand (Siliceous, hyperthermic Typic Psammaquents; Mu), Galveston-Mustang complex (GmB), and Lopeno (Mixed, hyperthermic Oxyaquic Ustipsamments) -Potrero (Mixed, hyperthermic Aquic Ustipsamments)-Arenisco (Mixed, hyperthermic Typic Ustipsamments) complex (LpC) (SSS n.d.).

2.2. Prescribed fire patches and treatments

Beginning in February 2016, sixteen burn patches ranging from 200 to 485 ha were burned with different season and return intervals (Fig. 2). All burn patches received an initial winter or summer burn treatment by summer 2019; repeat burns began in 2020. Season of treatment (winter burn, summer burn, no burn) and return interval (long or short) were randomly assigned (Table 1). Winter burn treatments were conducted during January or February; summer treatments were conducted during July or August. Short return interval patches were burned every 3 years; long return interval patches were burned every 5 years. For our study we used 2 × W16/21 (burned in winter 2016 and winter 2021), 3 × W19 (burned in winter 2019), 2 × W20 (burned in winter 2020), 2 × S16/21 (burned in summer 2016 and summer 2021), 2 × S19 (burned in summer 2019), 2 × S17/20 (burned in summer 2017 and summer 2020), and 3 × control (non-burned) patches.

Fuels were unprotected and most closely resembled fuel model GR 8 (Scott and Burgan, 2005) in Gulf cordgrass-dominated areas, and GR 6 or GR 7 in areas dominated by seacoast bluestem depending on recent rainfall and soil moisture. Weather conditions during burning were recorded every 30 min using a Kestrel® 5500 Weather Meter (Kestrel Instruments, Boothwyn, PA). Blacklining weather conditions generally fell within: temperature ≤32 °C, relative humidity 40–50 %, windspeeds

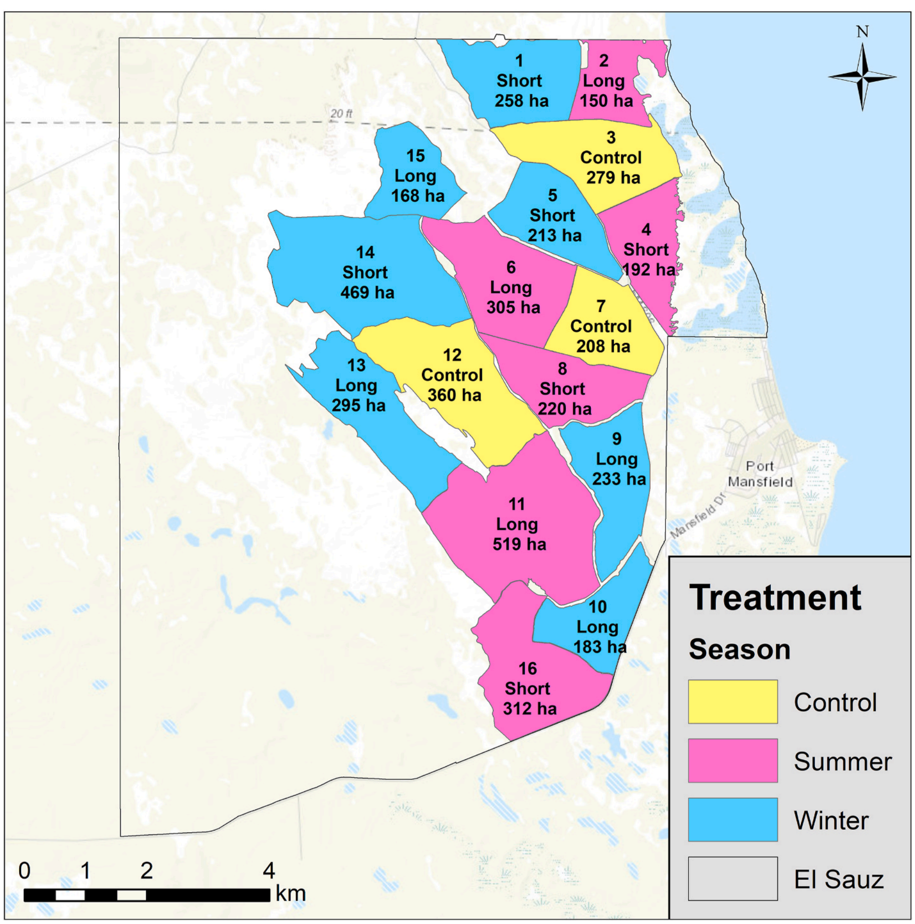

Fig. 2. Burning treatments assigned to patches at East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, 2020–2022. S = Summer, W = Winter, C = Control. 16/21 = Burned in 2016 then again in 2021, 17/20 = Burned in 2017 then again in 2020. 19 = Burned in 2019. 20 = Burned in 2020. Adapted from Zerlin et al., (2023).

Table 1
Prescribed burning treatment and size of burn patches at East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, 2020–2022 (as seen in Zerlin et al., 2023).

Patch ID #	Area (ha)	Season	Fire Return Interval	Initial Burn	Second Burn	Treatment
1	258	Winter	Short	Feb17	Feb20	W20
2	150	Summer	Long	Jul16	Aug21	S16/21
3	279	Control	NA	NA	NA	Control
4	192	Summer	Short	Aug17	Jul20	S17/20
5	213	Winter	Short	Feb17	Feb20	W20
6	305	Summer	Long	Jul16		S16/21
7	208	Control	NA	NA	NA	Control
8	220	Summer	Short	Aug17	Aug20	S17/20
9	233	Winter	Long	Feb16	Feb21	W16/21
10	183	Winter	Long	Feb16	Feb21	W16/21
11	519	Summer	Long	Sep19		S19
12	360	Control	NA	NA	NA	Control
13	295	Winter	Long	Feb19		W19
14	469	Winter	Short	Jan19	Feb22	W19
15	168	Winter	Long	Jan19		W19
16	312	Summer	Short	Sep19		S19

≤3.6 m/s, mixing height ≥488 m, although occasionally mixing heights were lower. Weather conditions for flanking fires were: temperature ≤38 °C, RH ≥ 25 %, sustained windspeeds 2.2–6.7 m/s with gusts up to 8.9 m/s, mixing height ≥488 m, although occasionally mixing heights were lower. For both blacklining and flanking fires, lighting began as soon as fine fuels were dry enough to carry fire, typically between 900 and 1000 (GMT -05:00). Blacklining typically was completed by 1400, and the burning of the interior of the patch by 1800.

2.3. *Butterfly sampling*

Four 100 m × 10 m belt transects were permanently marked with t-posts in each patch to form a square array. Burn patches near the coast included both Gulf cordgrass communities and mixed grass communities. In these patches, one sampling array was placed in each vegetation type. Burn patches further inland lacked Gulf cordgrass; one sampling array was placed in the mixed grass community. Sampling arrays were placed as close to the center of the patch, or the center of the vegetation community as possible. There were 24 sampling arrays in total.

Monthly walking butterfly surveys were completed on each array from March 2020 through February 2022 using a modified Pollard method (Pollard, 1977). Transects were walked at a pace of approximately 5 min per 100 m. Butterflies observed within the 100 m × 10 m belt transect were identified and recorded. Members of the Theclinae and Polyommatinae subfamilies, in the family Lycaenidae, were recorded only as "HAIR" and "BLUE," respectively, because of difficulty obtaining a positive identification at a lower taxonomic level. Other butterflies that we were unable to identify upon sight were caught with a butterfly net, identified, and released on-site. All species were identified by the same surveyor. Surveys took an average of three days a month, visiting approximately 8 transect arrays per day when weather conditions were met. In order to reduce driving time between transects, groups of transects were often visited within the same day: coastal transects located on the eastern portion of the ranch, inland transects located on the western portion of the ranch, and transects located in between the coastal and western portions were grouped together for sampling. Within groups, arrays were visited in random order.

Butterfly surveys occurred between the hours of 0900–1600 (fall and spring) and 0800 to 1700 (summer). Surveys were conducted when air temperature was above 17 °C, winds were below 4.5 mps, and cloud cover generally was <50 %. Time, windspeed, and temperature were recorded at the beginning and end of each butterfly survey; windspeed and temperature were recorded with a Kestrel® 5500 Weather Meter held at a 1.5 m height.

2.4. *Monarch tagging*

All monarchs we could catch were netted and tagged following Monarch Watch protocols (Monarch Watch n.d.) whether seen along a sampling transect or not. Tags (Monarch Watch, Wilmington, DE) were colored light blue and placed on the left hindwing to allow us to visually identify previously-tagged monarchs if they were seen again.

2.5. *Burn treatment analyses*

Effects of prescribed fire, time since prescribed fire, and their interactions on butterfly abundance were assessed by comparing the 3 winter burn treatment groups (W16/21, W19, W20) and the control treatment and the 3 summer burn treatment groups (S16/21, S19, S17/20) and the control treatment. We used a linear mixed model with treatment (season of burn), time since burn, and their interaction as fixed effects and a patch nested within treatment as a random effect. Time since burning was analyzed as a repeated measures effect with a patch nested within treatment as a subject. We used an information-theoretic criterion to select the most appropriate variance-covariance structure describing non-independence because of repeated measures (Ritzell et al., 2022). Data were analyzed on a log(Y+1) scale. Normality of residuals was assessed with the Shapiro and Wilk (1965) test. Results are presented on a back-transformed scale. When burning treatment and time since burning interacted, we compared treatments each month since burning (Kirk, 2013). Effect sizes were estimated with the partial eta-squared statistic ($\widehat{\eta}_p^2$) (Cohen, 1973; Lakens, 2013) as implemented by Tippey and Longnecker (2016) for mixed models; additionally, percent change between each treatment and the control is summarized for Lepidoptera results.

Butterfly diversity (richness, Shannon's index, and Simpson's index) was based on butterflies identified to the lower taxonomic level (subfamilies for HAIR and BLUE groups, species for others). Richness was analyzed on a log(Y + 1) scale and back-transformed for data presentation; normal scores (Mansouri and Chang, 1995) were analyzed for Shannon's and Simpson's indices because these indices are not normally distributed (Fritsch and Hsu, 1999; Rogers and Hsu, 2001). Several transects were removed from data analysis because they were disturbed during fire line construction, impacted by a December 2021 wildfire, or inaccessible because of local flooding.

2.6. *Motte distance*

To determine if the distance to woody motte impacted butterfly abundance on sampling arrays, the relationship between the total number of butterflies and distance from the center of the array to the closest motte in (non-burned) control patches was analyzed with a generalized linear regression using a log link that modeled the response variable distributed as a negative binomial random variable. The analysis tested for equality of slopes between cordgrass and non-cordgrass-dominated vegetation in the patches that had both herbaceous vegetation communities. The null hypothesis was that abundance of butterflies was not affected by distance to oak mottes in either herbaceous vegetation type.

3. Results

3.1. *Abundance*

We recorded 4889 individual butterflies from 44 species and 2 subfamilies that were not identified to species during our study (Table S1). This included individuals from all 6 butterfly families (Hesperiidae 442; Lycaenidae 1266; Nymphalidae 1560; Papilionidae 122; Pieridae 1472;

Riodinidae 7), and 20 unidentified individuals.

Summer burning treatment and sampling month interacted ($F_{60,\ 95.2} = 1.84$, $P = 0.0038$) in their effects on butterfly abundance (Fig. 3, Table S2). Burning effects were detected in six monthly sampling periods. In July 2020, more butterflies were observed in control treatments than in S19 ($t_{78.9} = 2.51$, $P = 0.0141$) (11 months after burning) and in S17/20 ($t_{78.9} = 2.17$, $P = 0.0331$) (35 months after burning) treatments; abundance, however, did not differ ($t_{78.9} < 1.89$, $P > 0.0628$) among patches that received a burn treatment. In August 2020, we observed fewer butterflies ($t_{78.9} > 2.83$, $P < 0.0005$) in S17/20, 36 months after burning, than in any other treatments. In November 2020, there were fewer butterflies in S19, 15 months after burning, than in S17/20 ($t_{78.9} = 2.76$, $P = 0.0072$) (39 months after burning) and in the control patches ($t_{78.9} = 2.42$, $P = 0.0180$). In both June 2021 and November 2021, we observed fewer butterflies in the S19 treatment, 21 and 26 months after burning, than in the other treatments ($t_{78.9} > 4.55$, $P < 0.0001$ and $t_{78.9} > 2.18$, $P < 0.0318$). Finally, in December 2021, there were more ($t_{78.9} > 2.04$, $P < 0.0444$) butterflies in S16/21 and S17/20, 3 months and 16 months after burning, respectively, than in control or S19 treatments, 27 months following burning.

Winter burn treatments and sampling month did not interact ($F_{60;\ 52.2} = 0.84$; $P = 0.7493$) in their effects on butterfly abundance (Fig. 4, Table S2). Additionally, abundance did not differ ($F_{3;\ 5.01} = 0.32$; $P = 0.813$) between burn and control treatments. There were differences in butterfly abundance, however, among sampling months ($F_{20;\ 52.2} = 16.87$; $P < 0.0001$).

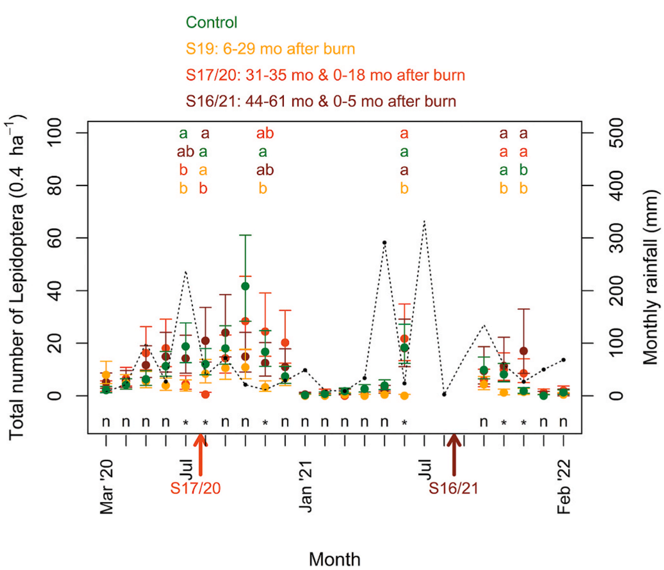

Fig. 3. Median (±se) monthly total abundance of butterflies in 3 summer burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. For treatment S19, these months represent 6–29 months post-burning in 2019; for treatment S17/20, these months represent 31–35 months post burning in 2017 and 0–18 months post-burning in 2020; for treatment S16/21, these months represent 44–61 months post-burning 2016 and 0–5 months post-burning in 2021. When treatment and month interacted but treatments did not differ within a month, an "n" is indicated; when treatments differed within a month, an asterisk (*) is indicated, and for these months, treatment medians with the same lower-case letter (suspended near the top of the graph and colored-coded by treatment) are not significantly different (P > 0.05, protected LSD test). Data were analyzed on a log(Y + 1) scale; back-transformed means estimated medians with asymmetric standard errors are presented. Arrows below the x-axis indicate when the S17/20 and S16/21 fires were conducted. July through September 2021 were not included in analyses because some patches were inaccessible due to flooding.

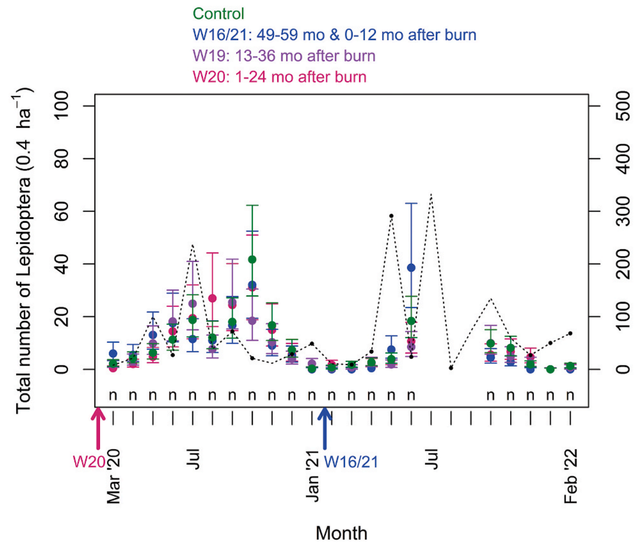

Fig. 4. Median (±se) monthly total abundance of butterflies in 3 winter burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. For treatment W16/21, these months represent 49–59 months post-burning in 2016 and 0–12 months post-burning in 2021; for treatment W19, these months represent 13–36 months post burning in 2019; for treatment W20, these months represent 1–24 months post-burning 2016 and 0–5 months post-burning in 2021. When treatment and month interacted but treatments did not differ within a month, an "n" is indicated; when treatments differed within a month, an asterisk (*) is indicated, and for these months, treatment medians with the same lower-case letter (suspended near top of graph and colored-coded by treatment) are not significantly different (P > 0.05, protected LSD test). Data were analyzed on a log(Y + 1) scale; back-transformed means estimated medians with asymmetric standard errors are presented. Arrows below the x-axis indicate when the W20 and W16/21 fires were conducted. July through September 2021 were not included in analyses because some patches were inaccessible due to flooding.

3.2. Plant community type

We compared butterfly abundance in the burn patches that supported both Gulf cordgrass and non-cordgrass, mixed grass community types. Within each of these treatments, butterfly abundance on cordgrass sampling arrays was compared to that on non-cordgrass arrays. There was no effect of plant community type in the W20 burning treatment ($F_{1;\ 2} = 0.19$; $P = 0.7066$), nor did community type interact with burning treatment ($F_{1;\ 2} = 4.03$; $P = 0.1824$), month of sampling ($F_{20,\ 80} = 0.40$; $P = 0.9882$), or their combination ($F_{20;\ 80} = 0.41$; $P = 0.9862$). Similarly, plant community type did not affect butterfly abundance in the S16/21 treatment ($F_{1;\ 1.86} = 1.86$; $P = 0.3139$), and community type did not interact with burning treatment ($F_{1;\ 1.86} = 0.01$; $P = 0.9361$), month of sampling ($F_{20,\ 70} = 0.98$; $P = 0.4993$), or their combination ($F_{20;\ 60} = 0.65$; $P = 0.8572$). S17/20 had an interaction between cordgrass and treatment ($F_{1;\ 2.01} = 9.30$; $P < 0.0063$), but when examining the simple main effects, there was no burn effect for either community type, cordgrass ($F_{1;\ 2.97} = 2.10$; $P > 0.2438$) and non-cordgrass ($F_{1;\ 2.97} = 1.31$; $P > 0.3355$). Overall, community type did not affect butterfly abundance.

3.3. Richness

Summer burn treatments interacted ($F_{60,95.2} = 1.9$, $P = 0.0025$) with month of sampling in their effects on richness (Fig. 5, bottom; Table S3). We detected no treatment effects ($F_{3,\ 73.7} \leq 2.54$, $P \geq 0.0632$) from March through June 2020. In July 2020, richness was higher in S16/21 burn ($t_{73.7} = 2.78$, $P = 0.0070$) (49 months post-burn) and control treatments ($t_{73.7} = 2.35$, $P = 0.0217$) than in the S19 burn (11 months

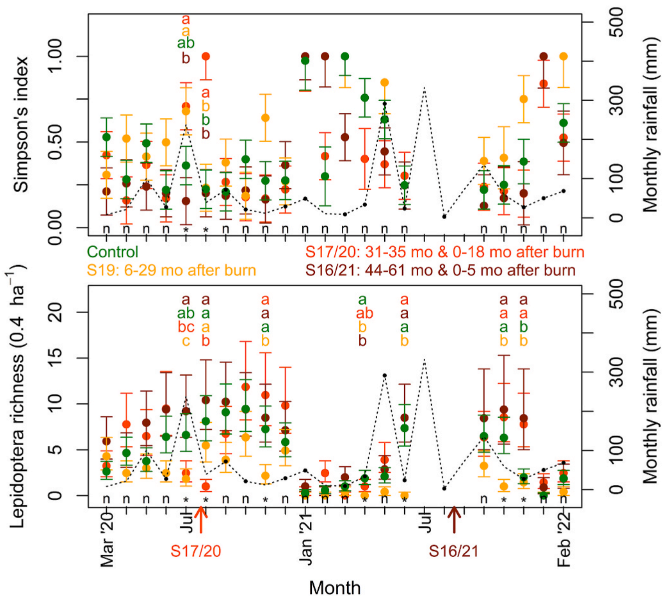

Fig. 5. Bottom: Mean (±se) monthly richness of butterflies in 3 summer burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. Top: Mean (±se) monthly Simpson's index of butterflies in 3 summer burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. For treatment S19, these months represent 6–29 months post-burning in 2019; for treatment S17/20, these months represent 31–35 months post burning in 2017 and 0–18 months post-burning in 2020; for treatment S16/21, these months represent 44–61 months post-burning 2016 and 0–5 months post-burning in 2021. When treatment and month interacted but treatments did not differ within a month, an "n" is indicated; when treatments differed within a month, an asterisk (*) is indicated, and for these months, treatment means with the same lower-case letter (suspended near top of graph and colored-coded by treatment) are not significantly different (P > 0.05, protected LSD test). Abundance data were analyzed on a log(Y + 1) scale; back-transformed means with asymmetric standard errors are presented. Normal scores were analyzed for Simpson's index; observed means and standard errors are presented; because the design was unbalanced, some estimated means exceeded 1 and these values were set to 1; upper mean + standard error whiskers greater than 1 are not shown. Arrows below the x-axis indicate when the S17/20 and S16/21 fires were conducted. July through.

after burning), and higher ($t_{73.7} = 2.34$, $P = 0.0222$) in the S16/21 treatment than in the S17/20 treatment (35 months post-burn). In the next month (August 2020), richness was higher and similar ($t_{73.7} \leq 1.22$, $P \geq 0.2253$) among S16/21, control, and S19 treatments but lower ($t_{73.7} \geq 2.54$, $P \leq 0.0130$) in the S17/20 treatment, immediately after burning, than in the other treatments. By November 2020, richness was lower ($t_{73.7} \geq 2.27$, $P \leq 0.0260$) in the S19 treatment (15 months after burning) than any other treatment. We detected no differences ($F_{3,73.7} \leq 2.58$, $P \geq 0.0632$) among treatments between December 2020 and March 2021. In April 2021, richness was higher in the control treatment than in S19 ($t_{73.7} = 2.51$, $P = 0.0142$) (19 months after burning) and S16/21($t_{73.7} = 2.51$, $P = 0.0142$) (57 months after burning) treatments, but similar ($t_{73.7} = 0.87$, $P = 0.3881$) between control and S17/20 (8 months after burning) treatments. In June 2020, richness was lower ($t_{73.7} \geq 4.87$, $P \geq 0.0001$) in the S19 burn (21 months after burning) than in the other treatments. In November 2021, richness was lower ($t_{73.7} \geq 2.96$, $P \leq 0.0039$) in the S19 treatment (26 months after burning) than in the other treatments; and in December 2021, richness was higher ($t_{\leq 90} \geq 2.19$, $P \leq 0.0130$) in S16/21 (3 months post-burn) and S17/20 (15 months post-burn) treatments than in control and S19 treatments (26 months post-burn).

Butterfly richness responded differently to winter burning than to summer burning—in particular, winter burning treatment had no effect ($F_{3,5} = 2.96$, $P = 0.1366$) on richness, nor did treatment interact ($F_{60,100} = 1.25$, $P = 0.1608$) with sampling month (Fig. 6, bottom, Table S3).

3.4. Shannon's and Simpson's indices

Summer burning treatments and month of sampling acted independently ($F_{60,74.1} = 1.38$, $P = 0.1001$) in their effects on Shannon's index (Table S3). Additionally, we detected no treatment effects ($F_{3,\ 5.05} = 2.28$, $P = 0.1954$). Similar patterns for Shannon's index were observed following winter burning: neither the treatment × sampling interaction ($F_{52,77} = 0.94$, $P = 0.5862$) nor the main effect of treatment ($F_{3,4.98} = 0.62$, $P = 0.6306$) were significant (Table S3).

Summer burning treatment and month of sampling interacted ($F_{52,\ 74.1} = 1.55$, $P < 0.0402$) in their effects on Simpson's index (Fig. 5, top). Butterfly dominance differed among summer burning treatments only during sampling months of July 2020 ($F_{3,\ 43.1} = 4.12$, $P < 0.0117$) and August 2020 ($F_{3,\ 43.1} = 4.36$, $P < 0.0091$). In July 2020, butterfly evenness did not differ ($t_{43.1} < 1.46$, $P > 0.1504$) among control, S17/20, and S19 treatments, and did not differ ($t_{43.1} = 1.90$, $P = 0.0647$) between C and S16/21; however, evenness was lower in S16/21 than in

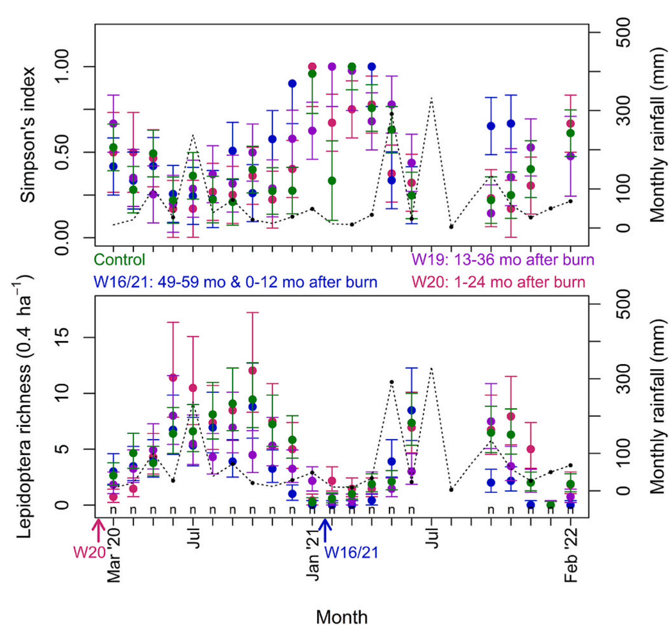

Fig. 6. Bottom: Mean (±se) monthly richness of butterflies in 3 winter burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. Top: Mean (±se) monthly Simpson's index of butterflies in 3 winter burning treatments and a non-burned control from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. For treatment W16/21, these months represent 49–59 months post-burning in 2016 and 0–12 months post-burning in 2021; for treatment W19, these months represent 13–36 months post burning in 2019; for treatment W20, these months represent 1–24 months post-burning 2016 and 0–5 months post-burning in 2021. When treatment and month interacted but treatments did not differ within a month, an "n" is indicated; when treatments differed within a month, an asterisk (*) is indicated, and for these months, treatment means with the same lower-case letter (suspended near the top of graph and colored-coded by treatment) are not significantly different (P > 0.05, protected LSD test). Abundance data were analyzed on a log (Y + 1) scale; back-transformed means with asymmetric standard errors are presented. Normal scores were analyzed for Simpson's index; observed means and standard errors are presented; because the design was unbalanced, some estimated means exceeded 1 and these values were set to 1; upper mean + standard error whiskers greater than 1 are not shown. Arrows below the x-axis indicate when the W20 and W16/21 fires occurred. July through September 2021 were not included in analyses because some patches were inaccessible due to flooding.

S17/20 ($t_{43.1} = 3.07$, $P = 0.0037$) and in S19 ($t_{43.1} = 2.99$, $P = 0.0046$) treatments. In August 2020, evenness was higher in S17/20 than in the other treatments ($t_{42.8} > 2.55$, $P < 0.0145$), with no differences ($t_{42.8} < 0.64$, $P > 0.5273$) among C, S16/21, and S19 treatments.

In contrast to summer burning results, burning and sampling month did not interact ($F_{52,\,77} = 1.00$, $P = 0.4900$) in their effects on Simpson's index for areas burned in winter. Additionally, we failed to detect ($F_{3,\,4.9} = 0.42$, $P = 0.7479$) a winter burning effect on Simpson's index (Fig. 6, top, Table S3). These results paralleled results for Shannon's index.

3.5. Monarch tagging

Thirty monarchs were observed, eight of which were caught and tagged (3 M:5 F). Most observations were fortuitous, occurring outside the formal butterfly surveys. All were observed in October or November, during peak southward migration. Monarchs were observed either flying, puddling, or nectaring. No tagged monarchs were recovered.

3.6. Distance to oak motte

The relationship between butterflies and distance from oak mottes in non-burned vegetation differed ($F_{1,16} = 9.83$, $P = 0.0064$) between Gulf cordgrass and non-cordgrass dominated plant communities (Fig. 7). In non-cordgrass communities, we did not detect ($\hat{\beta} = -0.00329 \pm 0.002548$, $t_{16} = -1.29$, $P = 0.2145$) a relationship between butterfly abundance and distance from oak mottes. In Gulf cordgrass-dominated areas, however, the total number of butterflies decreased by 19.6 % ($\hat{\beta} = -0.02182 \pm 0.005331$, $t_{16} = -4.09$, $P = 0.0008$) for each 10-m increase in distance from the nearest oak motte up to 100 m.

4. Discussion

4.1. Prescribed fire effects on butterfly populations

We observed an effect of time of year on butterfly abundance, richness, and diversity (both as indicated by Shannon's and Simpson's indices) regardless of treatment. This is not surprising because populations of butterfly species are ephemeral: they are present at different times throughout the year because of species-specific life cycles (Brock and Kaufman, 2003). We found no evidence that winter burn treatments

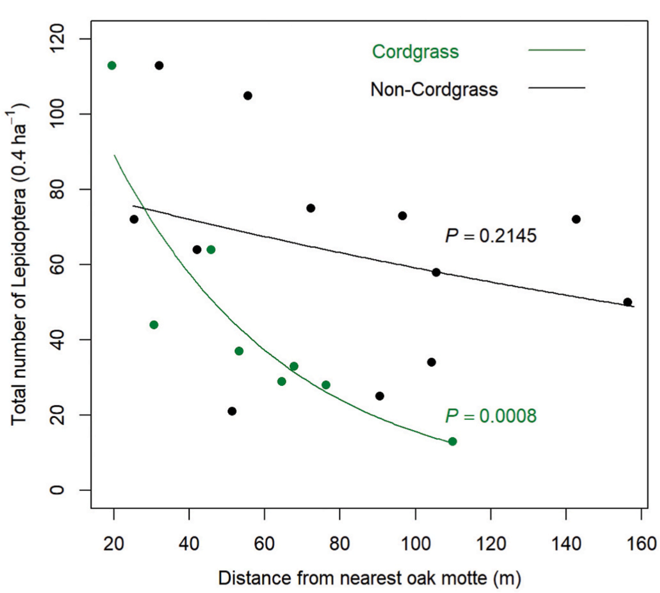

Fig. 7. Butterfly abundance as it relates to distance from nearest oak motte (m) from March 2020 through February 2022 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA.

impacted butterfly abundance, richness or diversity (by either Shannon's or Simpson's indices); in addition, we detected no effects of summer burning on diversity as measured by Shannon's index. However, summer burning affected species evenness (as indicated by Simpson's index) but this was an effect that was quite temporally-specific: summer burning affected evenness relations only during July 2020, when evenness was lower in control and S16/21 treatments than in S17/20 and S19 treatments, and in August 2020, when evenness was higher in S17/20 than in the other treatments.

There were several effects of summer burning on abundance or richness that lasted no longer than two consecutive months. Patterns in summer burn effects were difficult to discern with one exception. During months when there were differences, the S19 treatments often, but not always, resulted in lower abundance or lower richness than other treatments, even as long as 26 and 27 months after burning. In August 2020, both abundance and richness were lower in treatments that were burned the previous month, but they were not lower by September 2020, and there were no other instances when either abundance or richness was affected in the month immediately following burning.

Patterns of effects of burning on butterfly richness and diversity relations (as reflected in Shannon's and Simpson's indices) are difficult to generalize in our results. For example, with respect to summer burning, fire effects on richness were not uncommon (detected in 7 of 21 months)—and during these months, richness tended to be higher in S16/21 treatments relative to other treatments (in July and August 2020 and November and December 2021) but lower in April 2021. However, we detected no summer burning effects on Shannon's index, and whereas Simpson's index was lower (higher dominance) in treatments with lower richness during July and August 2020, no such patterns were evident during other months when richness was affected because Simpson's index was not affected during these months. No similar patterns were detected with respect to winter burning. Thus, our results provide little evidence that prescribed fire—whether during summer or winter seasons—had lasting effects on butterfly species richness or diversity relations (as reflected in Shannon's and Simpson's indices).

Adult butterflies are highly mobile. Schneider et al. (2003) studied the movement patterns of meadow brown (*Maniola jurtina* L.) and scarce copper (*Lycaenae virgaureae* L.) within a 172-ha area in Sweden. Meadow browns (n = 190) averaged 322 m between captures, while scarce coppers (n = 104) averaged 272 m between captures. They found that flower density was an important determining factor in the number of residents, emigrants, and immigrants of both species in various patches of pastures, meadows, intensively used grasslands, and other cover types, but larval host plant availability was not for scarce coppers. Interpatch distance was an important factor in the rate of emigration and immigration between various cover types. In our study, patches burned in summer were adjacent to patches of other treatments, allowing adult butterflies to move to more supportive habitat at will. Because our summer burn patches were burned late in the growing season, no flowering nectar plants would be available until the following spring.

We hypothesized that summer burning would have more positive impacts on butterfly populations than winter burning because burning in February in southern Texas can result in decreased forb yields (Hansmire et al., 1988). We reject that hypothesis. Additionally, we recognize that coastal southern Texas grasslands are somewhat unique in their latitude, growing season, and productivity, and include fairly rare vegetation types (Diamond et al., 2024). Our results may not apply to grasslands in other regions.

4.2. Impacts of weather

We were unable to access several of our burn patches in July, August, and September 2021 because of widespread local flooding. Thus, we were unable to compare immediate effects of burning that was conducted in August 2021. Although it is true that winter burning had no effect on butterflies, it is also true that there were very few butterflies recorded in our study during January, February, and March, even in the control patches.

Weather is known to impact butterfly populations (Pollard, 1988; Zerlin et al., 2023). Potentially beneficial impacts of precipitation include a subsequent increase in herbaceous vegetation that was documented on the Texas coast following Hurricane Harvey in 2017 (Ries et al., 2018). Port Mansfield, TX, approximately 4.4 km from the center of the ranch (Google Maps n.d.), received 721 mm of rain over the first year of our study (March 2020–February 2021). In July 2020, Hurricane Hanna, a Category 1 hurricane made landfall approximately 15 km north of our study site, bringing over 355 mm of rain to the ranch (Zerlin et al., 2023). In the second year of our study (March 2021–February 2022), Port Mansfield received 1132 mm of rain (PRISM, 2022). From 1981 to 2010, average annual precipitation at Port Mansfield was 657.8 mm (U.S. Climate Data n.d.). If higher rainfall dampened effects of burning on vegetation, this might, in turn, have reduced putative effects on butterflies (e.g., Dollar et al., 2013). Furthermore, effects of rainfall on butterfly abundance depend on species (e.g., Comay et al., 2021), and these effects may be masked in our analysis that considered total number of butterflies and diversity metrics.

4.3. Season of burning impacts

We expected higher butterfly diversity and abundance following summer burning than winter burning because winter burning can reduce forb populations (Hansmire et al., 1988). Given the structure of our treatments, a formal test of this hypothesis is not possible. However, mean butterfly abundance averaged 8.65 in summer-burned patches and 9.5 in winter-burned patches. Our results suggested little difference in summer- and winter-burned coastal grasslands.

More immediately, however, we also expected lower butterfly abundance and diversity following fire—regardless of season of burning—because fire removes food resources and shelter. Although adult butterflies can move to avoid fire, less mobile life cycles (eggs, pupae, caterpillars) are more susceptible to fire-induced mortality. For example, Thom et al. (2015) reported complete mortality of the Atala hairstreak pupae (*Aumaeus atala* [Poey]) at the soil level, whereas pupae buried at soil depths greater than 1.75 cm had better chances of survival. We found no evidence that winter burning affected butterfly abundance, diversity or richness. Furthermore, the few effects of summer burning that we detected were detrimental but were also short-lived (<2 mo).

A study of egg laying preferences of female monarch butterflies, both in the field and the laboratory, determined that butterflies laid more eggs on young plants or plants with newer leaf growth (Zalucki and Kitching, 1981). Jaumann and Snell-Rood (2017) studied 33 female cabbage white butterflies (*Pieris rapae*) that were reared in a laboratory from wild-caught mothers. These butterflies were provided their choice of host plants that received either high or low levels of fertilization. Butterflies laid more eggs on host plant leaves with higher nutrient content and conspecific density. Haynes et al. (2023) found that nutritional quality in the form of increased crude protein and decreased neutral detergent fiber occurred immediately after burning following both winter and summer burning at our study site, and abundant rainfall during our study allowed for immediate regrowth of nutritious herbaceous plants. This would partially explain immediate attraction of butterflies to recently burned areas and the short-lived duration of reductions in butterfly abundance that occurred in a few instances following summer burning.

4.4. Monarch butterflies

During the fall monarch butterfly migration in Texas most monarch butterflies have been observed migrating further inland (Journey North n.d.). The presence of monarchs at our site during October and November confirms that a small population of monarch butterflies is utilizing the coastal route at least as far south as Port Mansfield to migrate to the overwintering grounds in Mexico.

4.5. Woody mottes

Little research has been conducted on ecology of woody mottes in southern Texas. We observed an effect of woody mottes in Gulf cordgrass rangelands, where butterfly abundance was greater closer to mottes. The woody vegetation within these mottes serves as host plants for some butterfly species, provides nighttime roosts in their bark, and provides shade and cooler temperatures in extreme heat (Clench, 1966; Burrow et al., 2001; Olsen et al., 2018; Palmer et al., 2021); thus, resources located near and within mottes may be more desirable than the vegetation located farther away in rangelands dominated by Gulf cordgrass. Franzén et al. (2024) found that dense forests were less preferred by three threatened butterfly species than open grasslands that provide more sustenance, opportunities to find mates, and areas for oviposition through increased visibility. In our study, overall butterfly abundance was neither greater nor smaller in grasslands dominated by Gulf cordgrass compared to other areas; however, the edges of woody mottes in Gulf cordgrass areas proved to be valuable habitat for butterflies, supporting varied needs.

4.6. Management implications

Providing areas of non-burned vegetation within and adjacent to burned areas can provide protected space from which pollinators and other arthropods can recolonize burned areas (Harper et al., 2000; Panzer, 2002; Swengel and Swengel, 2007). Because (1) the few fire effects on butterflies we detected lasted less than two consecutive months, and (2) it is unlikely that this vegetation could support fire return intervals more frequent than every 12 months, it is unlikely that managers can burn too frequently to prevent pollinators to recolonize a disturbed area. Season of burn may impact arthropods because it influences effects on vegetation (Britton et al., 2010; Weir and Scasta, 2017), but it is also important to consider the impact of season of burning directly on arthropods in various life stages (Johnson et al., 2008). Providing a variety of time since burning, season of burning, and grazing intensity through a patch-burn grazing system can support diverse butterfly communities by providing for varied needs among species (Geest et al., 2023). Human health hazards (heat exhaustion and heat stroke) associated with extreme heat of summer burning in the southern United States (Wade and Lunsford, 1989) are also important considerations when planning prescribed burning in southern Texas.

Woody mottes within burned patches likely offered refugia for butterflies, allowing them to recolonize burned patches immediately following burning. We recommend that woody mottes be maintained in rangelands of coastal southern Texas because they provide important refugia from prescribed fires as well as extreme heat during summer months.

5. Conclusions

This study examined butterfly responses to burning over two years, with two seasons of burning and time-since-burning varying from 0 to 61 months. Our findings indicate that neither summer nor winter burning had significant detrimental effects on butterfly populations in coastal southern Texas. However, we recommend winter burning over summer burning because winter burning had no negative effects on butterfly populations and avoids the dangers associated with summer's extreme heat to the burning crew. More long-term studies of prescribed burning effects on butterflies in rangelands in a variety of seasons, locations, and precipitation patterns are needed to fully understand the relationship between prescribed fire and butterflies in rangelands.

CRediT authorship contribution statement

Rebecca R. Zerlin: Writing – original draft, Investigation, Funding acquisition, Data curation. **Juan C. Elissetche:** Writing – review & editing, Investigation, Data curation. **J. Silverio Avila-Sanchez:** Writing – review & editing, Investigation, Data curation. **Richard J.W. Patrock:** Writing – review & editing, Methodology. **David B. Wester:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Sandra Rideout-Hanzak:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Consent for publication

The Caesar Kleberg Wildlife Research Institute and East Foundation consented to publication. This is publication number 24–111 of the Caesar Kleberg Wildlife Research Institute and 105 of the East Foundation.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.128034.

Data availability

Data will be made available on request.

References

Ansley, R.J., Castellano, M.J., 2006. Strategies for savanna restoration in the southern great plains: effects of fire and herbicides. Restor. Ecol. 14 (3), 420–428. https://doi.org/10.1111/j.1526-100X.2006.00150.x.

Butterflies and Moths of North America (BAMONA). n.d. "Butterflies of United States." Accessed October 19, 2022. https://www.butterfliesandmoths.org/checklists?species_type=0&tid=45152.

Beasom, S.L., Haucke, H.H., 1975. A comparison of four distance sampling techniques in South Texas live oak mottes. J. Range Manag. 28 (2), 142–144. https://doi.org/10.2307/3897447.

Britton, C.M., Rideout-Hanzak, S., Brown, S.D., 2010. Effects of burns conducted in summer and winter on vegetation of Matagorda Island. Texas. Southwest. Naturalist 55 (2), 193–202. https://doi.org/10.1894/JB-07.1.

Brock, J.P., Kaufman, K., 2003. Field Guide of Butterflies of North America. Houghton Mifflin Company.

Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. J. Environ. Manag. 65 (1), 135–152. https://doi.org/10.1006/jema.2002.0540.

Brown, J.K., Smith, J.K. (Eds.), 2000. Wildland Fire in Ecosystems: Effects of Fire on Flora, vol. 2. Rocky Mountain Research Station, U.S. Forest Service. RMRS-GTR-42-vol.

Burrow, A.L., Kazmaier, R.T., Hellgren, E.C., Ruthven III, D.C., 2001. Microhabitat selection by Texas Horned Lizards in Southern Texas. J. Wildl. Manag. 65 (4), 645–652. https://doi.org/10.2307/3803015.

Carbone, L.M., Tavella, J., Pausas, J.G., Aguilar, R., 2019. A global synthesis of fire effects on pollinators. Global Ecol. Biogeogr. 28 (10), 1487–1498. https://doi.org/10.1111/geb.12939.

Ceballos, G., Davidson, A., List, R., Pacheco, J., Manzano-Fischer, P., Santos-Barrera, G., Cruzado, J., 2010. Rapid decline of a grassland system and its ecological and conservation implications. PLoS One 5 (1), e8562. https://doi.org/10.1371/journal.pone.0008562.

Clench, H.K., 1966. Behavioral thermoregulation in butterflies. Ecology 47 (6), 1021–1034. https://doi.org/10.2307/1935649.

Cohen, J., 1973. Eta-squared and partial eta-squared in fixed factor ANOVA designs. Educ. Psychol. Meas. 33 (1), 107–112.

Comay, O., Yehuda, O.B., Schwartz-Tzachor, R., Benyamini, D., Pe'er, I., Ktalav, I., Pe'er, G., 2021. Environmental controls on butterfly occurrence and species richness in Israel: the importance of temperature over rainfall. Ecol. Evol. 11, 12035–12050. https://doi.org/10.1002/ece3.7969.

Davis, A.K., Chi, J., Bradley, C., Altzier, S., 2012. The redder the better: wing color predicts flight performance in monarch butterflies. PLoS ONE 7 (7), e41323. https://doi.org/10.1371/journal.pone.0041323.

Diamond, D.D., Elliott, L.F., Sunde, M., 2024. Ecological systems of the South Texas Coast. Southwest. Nat. 68 (2), 100–111. https://doi.org/10.1894/0038-4909-68.2.100.

Dollar, J.G., Riffell, S.K., Burger Jr., L.W., 2013. Effects of managing semi-natural grassland buffers on butterflies. J. Insect Conserv. 17, 577–590.

Feber, R.E., Smith, H., MacDonald, D.W., 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. J. Appl. Ecol. 33 (5), 1191–1205. https://doi.org/10.2307/2404698.

Franzén, M., Askling, J., Kindvall, O., Johansson, V., Sunde, J., Forsman, A., 2024. Landscape properties and density dependence shape the movement patterns of three threatened butterflies. Landsc. Ecol. 39, 160. https://doi.org/10.1007/s10980-024-01963-4.

Fritsch, K.S., Hsu, J.C., 1999. Multiple comparison of entropies with application to dinosaur biodiversity. Biometrics 55 (4), 1300–1305. https://doi.org/10.1111/j.0006-341X.1999.01300.x.

Geest, E.A., Moranz, R.A., Baum, K.A., 2023. Patch-burn management affects grassland butterfly communities in cattle-grazed rangelands. Insect Conservation and Diversity 16 (4), 508–520. https://doi.org/10.1111/icad.12641.

Google Maps. n.d. Accessed April 14, 2023. https://www.google.com/maps/@26.5594555,-97.4911284,14513m/data=!3m1!1e3.

Gould, F.W., Hoffman, G.O., Rechenthin, C.A., 1960. Vegetational areas of Texas, Texas A&M University. Tex. Agric. Exp. Stn. Leafl. 492.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12 (10). https://doi.org/10.1371/journal.pone.0185809.

Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W., Jongehans, E., 2019. Declining abundance of beetles, moths and caddisflies in the Netherlands. Insect Conservation and Diversity 13, 127–139. https://doi.org/10.1111/icad.12377.

Hanberry, B.D., DeBano, S.J., Kaye, T.N., Rowland, M.M., Hartway, C.R., Shorrock, D., 2021. Pollinators of the Great plains: disturbances, stressors, management, and research needs. Rangel. Ecol. Manag. 78, 220–234. https://doi.org/10.1016/j.rama.2020.08.006.

Hansmire, J.A., Drawe, D.L., Wester, D.B., Britton, C.M., 1988. Effect of winter burns on forbs and grasses of the Texas coastal prairie. Southwest. Nat. 33 (3), 333–338. https://doi.org/10.2307/3671761.

Harper, M.G., Dietrich, C.H., Larimore, R.L., Tessene, P.A., 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. Nat. Area J. 20 (4), 325–335.

Haynes, V.L., Ávila-Sánchez, J.S., Toomey, A.E., Ortega-S, J.A., Campbell, T.A., Ortega-S Jr., A., Rideout-Hanzak, S., Wester, D.B., 2023. Patch burning improves nutritional quality of two gulf Coast grasses—And winter burning is better than summer burning. Fire 6, 105. https://doi.org/10.3390/fire6030105.

Hays, M., 1994. South Dakota prairies. https://www3.northern.edu/natsource/HABITATS/Sdprai1.htm. (Accessed 12 December 2021).

IPBES, 2019. Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Version 1). Zenodo. https://doi.org/10.5281/zenodo.3831673.

Jaumann, S., Snell-Rood, E.C., 2017. Trade-offs between fecundity and choosiness in ovipositing butterflies. Anim. Behav. 123, 433–440. https://doi.org/10.1016/j.anbehav.2016.11.011.

Johnson, S.D., Horn, K.C., Savage, A.M., Windhager, S., Simmons, M.T., Rudgers, J.A., 2008. Timing of prescribed burns affect abundance and composition of arthropods in the Texas Hill Country. Southwest. Nat. 53 (2), 137–145. https://www.jstor.org/stable/20424908.

Journey North. n.d. Monarch adult sighted. https://maps.journeynorth.org/map/?map=monarch-adult-fall&year=2021. (Accessed 14 January 2022).

Jue, D.K., Merwin, A.C., Jue, S.S., McElveen, D., Inouye, B.D., 2022. Effects of frequency and season of fire on a metapopulation of an imperiled butterfly in a longleaf pine forest. Conservation Science and Practice:e12739. https://doi.org/10.1111/csp2.12739.

Kirk, R.E., 2013. Experimental Design: Procedures for the Behavioral Sciences. Sage Publications, California. https://doi.org/10.4135/9781483384733.

Ladybird Johnson Wildflower Center, 2022. Plant database. Quercus virginiana. Last updated 5 Nov. 2015. https://www.wildflower.org/plants/result.php?id_plant=QUVI.
Lakens, D., 2013. Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. Front. Psychol. 4, 863.
Mansouri, J., Chang, G.-H., 1995. A comparative study of some rank tests for interaction. Comput. Stat. Data Anal. 19, 85–96.
Monarch Watch. n.d. Tagging monarchs. Accessed May 15, 2022. https://monarchwatch.org/tagging/.
New, T.R., Pyle, R.M., Thomas, J.A., Thomas, C.D., Hammond, P.C., 1995. Butterfly conservation management. Annu. Rev. Entomol. 40, 57–83. https://doi.org/10.1146/annurev.en.40.010195.000421.
National Oceanic and Atmospheric Association (NOAA). N.d. normal monthly station details for port mansfield. https://www.ncdc.noaa.gov/cdoweb/datasets/NORMAL_MLY/stations/. (Accessed 7 October 2015).
Olsen, B.R.J., Fulbright, T.E., Hernández, F., Grahmann, E.D., Wester, D.B., Hehman, M.W., 2018. Ground surface vs. black globe temperature in northern bobwhite resource selection. Ecosphere 9 (9), e02441. https://doi.org/10.1002/ecs2.2441.
Palmer, B.J., Fulbright, T.E., Grahmann, E.D., Hernández, F., Hehman, M.W., Wester, D.B., 2021. Vegetation structural attributes providing thermal refugia for northern bobwhites. J. Wildl. Manag. 85 (3), 543–555. https://doi.org/10.1002/jwmg.22006.
Panzer, R., 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conserv. Biol. 16 (5), 1296–1307. https://www.jstor.org/stable/3095325.
PRISM, 2022. Time series data. Dataset: AN81m. Location: Lat 26.5498. Lon -97.4571. http://www.prism.oregonstate.edu/documents/PRISM_datasets.pdf. (Accessed 14 April 2023).
Pollard, E., 1977. A method for assessing changes in the abundance of butterflies. Biol. Conserv. 12 (2), 115–134. https://doi.org/10.1016/0006-3207(77)90065-9.
Pollard, E., 1988. Temperature, rainfall, and butterfly numbers. J. Applied Ecology 25 (3), 819–828. https://doi.org/10.2307/2403748.
Ries, L., Neupane, N., Baum, K.A., Zipkin, E.F., 2018. Flying through hurricane central: impacts of hurricanes on migrants with a focus on monarch butterflies. Anim. Migrat. 5, 94–103. https://doi.org/10.1515/ami-2018-0010.
Ritzell, A.D., Hernandez, F., Edwards, J.T., Montalvo, A., Wester, D.B., Grahmann, E.D., Rollins, D., Stewart, K.G., Smith, R.A., Woodard, D.A., Brennan, L.A., 2022. Quail and rain in semiarid rangelands: does management matter? J. Wildl. Manag. https://doi.org/10.1002/jwmg.22209.
Rogers, J.A., Hsu, J.C., 2001. Multiple comparisons of biodiversity. Biom. J. 43 (5), 617–625. https://doi.org/10.1002/1521-4036(200109)43:5<617::AID-BIMJ617>3.0.CO;2-J.
Schneider, C., Dover, J., Fry, G.L.A., 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecol. Entomol. 28, 219–227. https://doi.org/10.1046/j.1365-2311.2003.00494.x.
Scott, J.H., Burgan, R.E., 2005. Standard Fire Behavior Fuel Models: a Comprehensive Set for Use with Rothermel's Surface Fire Spread Model. Rocky Mountain Research Station, U.S. Forest Service. RMRS-GTR-153.
Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611.
Soil Survey Staff (SSS). n.d. Web soil survey. Accessed 5 June 2017. https://websoilsurvey.sc.egov.usda.gov/.
Stambaugh, M.C., Sparks, J.C., Abadir, E.R., 2014. Historical pyrogeography of Texas, USA. Fire Ecology 10 (3), 72–89. https://doi.org/10.4996/fireecology.1003072.
Swengel, S.R., Schlicht, D., Olsen, F., Swengel, A.B., 2011. Declines of prairie butterflies in the midwestern USA. J. Insect Conserv. 15, 327–339. https://doi.org/10.1007/s10841-010-9323-1.
Swengel, A.B., Swengel, S.R., 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. J. Insect Conserv. 11, 263–279. https://doi.org/10.1007/s10841-006-9042-9.
Thom, M.D., Daniels, J.C., Kobziar, L.N., Colburn, J.R., 2015. Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. PLoS One 10 (5). https://doi.org/10.1371/journal.pone.0126755.
Tippey, K.G., Longnecker, M.T., 2016. An ad hoc method for computing pseudo-effect size for mixed models. In: Proceedings of South Central SAS Users Group Forum.
U.S. Climate Data. n.d. Climate port mansfield – texas. https://www.usclimatedata.com/climate/port-mansfield/texas/united-states/ustx1077. (Accessed 25 October 2022.).
Van Nuland, M.E., Haag, E.N., Bryant, J.A.M., Read, Q.D., Klein, R.N., Douglas, M.J., Gorman, C.E., Greenwell, T.D., Busby, M.W., Collins, J., LeRoy, J.T., Schuchmann, G., Schweitzer, J.A., Bailey, J.K., 2013. Fire promotes pollinator visitation: implications for ameliorating declines of pollination services. PLoS One 8 (11). https://doi.org/10.1371/journal.pone.0079853.
Wade, D.D., Lunsford, J.D., 1989. A Guide for Prescribed Fire in Southern Forests. Southern Research Station, U.S. Forest Service. R8-TP-11.
Weir, J.R., Scasta, J.D., 2017. Vegetation responses to season of fire in tallgrass prairie: a 13-year case study. Fire Ecology 13 (2), 137–142. https://doi.org/10.4996/fireecology.130290241.
Zalucki, M.P., Kitching, R.L., 1981. Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, *Asclepias* spp. J. Zool. (Oxf.) 198 (1), 103–116. https://doi.org/10.1111/j.1469-7998.1982.tb02063.x, 10.1111/j.1469-7998.1982.tb02063.x.
Zerlin, R.R., Elissetche, J.C., Campbell, T.A., Patrock, R.J., Wester, D.B., Rideout-Hanzak, S., 2023. Extreme weather impacts on butterfly population in southern Texas, USA. J. Insect Conserv. 28, 89–102. https://doi.org/10.1007/s10841-023-00525-4.