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ORIGINAL PAPER

Extreme weather impacts on butterfly populations in Southern Texas, USA

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Abstract
Climate change is altering biodiversity of ecosystems worldwide by causing shifts in species' home ranges, potential extinctions of species, and Extreme Climatic Events (ECEs), such as hurricanes and extreme temperatures. The purpose of this study was to examine effects of two extreme weather events on butterfly populations in the Gulf Prairies and Marshes ecoregion in Willacy and Kenedy Counties, TX, USA. These weather events occurred during an ongoing study of effects of prescribed burning during summer or winter on butterfly populations. We tested effects of Category 1 Hurricane Hanna by comparing butterfly abundance in the month prior to and following the hurricane (July and August 2020). We tested effects of Winter Storm Uri by comparing butterfly abundance in the three months following the storm (March through May 2021) with abundance during the same period in the previous year (March through May 2020). We measured no effect of the Category 1 hurricane on butterfly populations overall and across all prescribed fire regimes. There was a significant reduction in butterfly abundance following the 2021 winter storm, and effects depended on prescribed fire regime. Our findings indicate that extremely cold temperatures in subtropical regions will likely have greater negative effects on butterfly populations than low-magnitude hurricanes.

Implications for insect conservation With extreme climate events (ECEs) predicted to increase in the future, measures should be taken to provide protection and refugia for butterflies, particularly from prolonged, uncharacteristically low temperatures. Protection includes maintaining undisturbed areas with accumulated plant matter, in preparation for these unpredictable events.

Keywords Abundance · Butterfly · Climate · Freeze · Hurricane

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Introduction

Climate change is altering ecosystems worldwide, and many species are being forced to adapt to these changes because of their effects on food resources, modifications to habitat, and changes in weather patterns (IPBES 2019; IPCC 2021). These changes will impact biodiversity by causing shifts in home ranges, pushing some species poleward or into higher elevations or by causing extinctions of other species (HilleRisLambers et al. 2013).

The earth's temperature has increased by 1 °C since pre-industrial times and is expected to continue to increase (Raven and Wagner 2021). Increasing temperature can lead to alterations in habitat suitability for plants (Anderson and Song 2020) and wildlife (LeDee et al 2020). Climate change will also lead to Extreme Climatic Events (ECEs), such as more frequent hurricanes, droughts, heavy rainfall, and

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extreme temperatures (Bell et al. 2018; Myhre et al. 2019; Tabari 2020; IPCC 2021). It is important to examine the impact ECEs have on flora and fauna in impacted areas.

In Texas, expected impacts of climate change include warmer weather, increased wildfires, coastal land loss and increased inland flooding, and increased impact from hurricanes (Banner et al. 2010; Zhao et al. 2016). These may become problems for many species because Texas is ranked in the top five states in the United States in terms of biodiversity (Stein 2002). Texas' high species diversity is a product of both its size and its location relative to equator and the Gulf of Mexico, which allow for a variety of habitat types and species. Many of these species include insects, which can be affected by climate change (Eigenbrode et al. 2022).

Insects have relatively short lifecycles, and can be very useful in investigating impacts of ECEs. Although insect communities may naturally vary seasonally because of weather patterns and changes in food availability, there has been a general trend in declining insect populations worldwide (Hallman et al. 2017; Raven and Wagner 2021).

Hallman et al. (2017) reported over a 75% decline in flying insects in nature reserves and protected areas over the span of 27 years in Germany. A related study by Hallmann et al. (2019) also recorded declines in biomass of beetles, moths, and caddisfly in the Netherlands over a 27-year period. European countries have also experienced declines specifically in butterfly populations (Warren et al. 2021). Similar trends have been reported in the United States as well, such as the decline of native bees and beetles as a result of multiple stressors including climate change (Halsch et al. 2021; Wagner et al. 2021).

Because insects are highly variable—they are the most diverse form of multi-cellular terrestrial animals—not all insect species respond in the same manner to climate change. Although many species of insects have been experiencing population declines, there are some species that will benefit from climate change. Warren et al. (2021) reported that climate change can have both positive and negative effects on butterflies, because warmer temperatures can allow some species to immigrate seasonally, or even year-round, to historically cooler areas that they would not have previously inhabited. Crossley et al. (2020) reported mixed results in insect and other arthropod diversity and abundance over time in different monitoring sites throughout the United States; some insect species declined but other insect species' populations either increased or remained unchanged during the study period. Despite variability among species, general trends indicate a 1–2% yr^{-1} decline in insect abundance (Wagner et al. 2021).

The order Lepidoptera includes butterflies and moths and is the second largest order of insects following Coleoptera. Lepidoptera are found in every terrestrial biome, with the exception of those in Antarctica (Ahmed et al. 2015). Out of the 853 species of butterflies found in North America, over 400 species and subspecies have been observed in Texas, the most of any of the United States (Quinn and Klym 2009). Within Texas, 481 species of butterflies have been observed in the lower Rio Grande Valley (BAMONA 2022). Cameron, Starr, and Hidalgo Counties of Texas have the greatest diversity because they are closest to the equator and located in the Rio Grande Valley. Butterflies are often the subjects of surveys because they are easily noticed and can often be identified in flight, making them ideal survey species. Because of their host plant requirements and short lifespans, it has been argued that butterflies are ideal bio-indicator species to evaluate habitat conditions (Syaripuddin et al. 2015).

As with many insect species, studies have shown mixed results of the impacts of climate change on Lepidopteran species. Forister et al. (2021) examined three butterfly datasets ranging from 15–48 years spanning the western United States and reported a 1.6% annual reduction in the number of individual butterflies over a 40-year period, especially with warming fall months. Wepprich et al. (2019) recorded an annual 2% decline in overall butterfly abundance over a 20-year monitoring period across the state of Ohio, matching trends observed in Europe. There were a few species that experienced increases in abundance over the course of monitoring such as the Zebra swallowtail (*Eurytides marcellus*), the Least skipper (*Ancyloxypha numitor*), and the Northern pearly-eye (*Enodia anthedon*). Forister et al. (2010) also reported an increase in butterfly richness and abundance in higher elevation sites in the Sierra Nevada Mountains of the western United States over a 35-year period. As with all insects, butterfly declines are multi-faceted, and there may be multiple causes of declines in populations.

Climate change has been predicted to lead to warmer temperatures, especially warming oceans in areas such as the North Atlantic (IUCN 2017). This warmer water is ideal for hurricane formation and can likely lead to an increase in hurricane activity for the North Atlantic (IUCN JM 2016; Trenberth et al. 2018). The length of time that ocean waters remain warm is also increasing and this, in turn, has led to an increase in hurricane season length. The U.S. National Climate Assessment in 2014 reported an increase in intensity, frequency, and duration of North Atlantic hurricanes since the 1980s (USGCRP 2014). With hurricanes expecting to increase in intensity because of climate change, coastal Texas can be expected to experience more frequent hurricanes in the future.

The Florida Keys experience tropical weather impacts. Salvato and Salvato (2007) examined the impact of four major hurricanes on butterflies in Florida. They recorded decreases in richness and abundance following storms; recovery appeared to be related to host and nectar plant availability. Certain species, however, experienced total disappearance or delayed recovery post-storms. These results indicate that hurricane activity may have adverse impacts on butterflies' lifecycles.

Although climate change is known for creating hotter temperatures overall, it may also bring about cooler temperatures and increased precipitation in localized areas (Morss et al. 2011). This can be disruptive to butterflies and other insects because they can be sensitive to colder temperatures. Some insect species have adaptations that allow them to survive winter temperatures depending on their location and life stage during winter (Turnock and Fields 2005; Bale and Hayward 2010). However, changes in winter climates can cause catastrophic effects on insects that are not equipped to deal with them, especially insects located in tropical or subtropical environments. In January 1981, a 10-day period of unusual winter weather occurred in the central highlands of Michoacan, Mexico. It included daily rain and hail that impacted overwintering monarch (*Danaus plexippus*) butterflies, and brought three days of snow to the region. Behavior that normally protected the butterflies from inclement weather, such as high roosting and climbing up to low vegetation, was only partially effective. Butterflies were dislodged from the branches of trees in which they were roosting, and many were buried under snow on the forest floor. The combination of soaking rain, hail, and freezing temperatures resulted in 2.5 million monarchs dying in this one extreme weather event (Calvert et al. 1983). Not only can low temperatures impact butterflies directly, but indirect impacts may also include destruction of important host plants, as in the case of a 2010 cold weather event in Everglades National Park, Florida. The park experienced two weeks of record low temperatures that fell into 5 °C in the evenings, with a low of −2.0 °C in January, causing frost damage for pineland croton (*Croton cascarilla*), a host plant for the Florida Leafwing butterfly (*Anaea troglodyta floridalis*) (Hallac et al. 2010).

Climate change is expected to cause increased temperature variability during winter (Francis and Vavrus 2012). These fluctuating temperatures may lead to population declines for invertebrates not equipped to handle the changes, such as Rocky Mountain parnassian (*Parnassius smintheus*) which exhibited population declines with both extremely cold or extremely warm winters in Alberta, Canada (Roland and Matter 2013).

Objective

In March 2020, we began a study of prescribed burning effects on butterfly populations in coastal southern Texas. In July 2020, Hurricane Hanna directly hit our study area. Five months later, in February 2021, Texas experienced Winter Storm Uri with temperatures falling below freezing for most of the state. Our primary objective is to examine the effects of these two consecutive extreme weather events—a Category 1 hurricane and a historic winter storm—on butterfly populations in coastal southern Texas. The purpose of this paper is not to report effects of prescribed burning on butterfly populations. However, because our study of extreme weather events is overlaid onto a study of varied prescribed fire regimes, it would be naïve to assume that fire regime had no impact on the effects of extreme weather events on butterflies, thus we have examined these weather effects in the context of our fire regimes. Our second objective is to determine if prescribed fire regime impacted the effects of the extreme weather events. We hypothesized that both the hurricane and the winter storm would negatively impact butterfly populations, and that prescribed burning would impact those effects.

Hurricane Hanna

Hurricane Hanna was the first hurricane to make landfall in the United States for the 2020 Hurricane season. First forming as an area of low pressure on 22 July 2020, Hanna officially became a tropical storm on 24 July and continued intensifying as it approached the Texas coast. Hanna made landfall on the evening of 25 July 2020, undergoing rapid intensification into a Category 1 hurricane with maximum sustained winds of approximately 144 kph and peak gusts of 167 kph (NOAA 2020; NWS Corpus Christi 2020). The first landfall was approximately 18 km north of Port Mansfield, Texas, USA on uninhabited Padre Island, a barrier island along the Gulf Coast of Texas. Second landfall was declared in eastern Kenedy County, Texas, once Hanna passed over the Laguna Madre. Including post-hurricane feeder bands, Port Mansfield received over 355 mm of rain and experienced winds between 129–137 kph (NOAA 2020). Port Mansfield is approximately 3.2 km southeast of our study site. From 1981 to 2010, historic average precipitation at Port Mansfield for the month of July was 61.7 mm, average annual precipitation was 657.8 mm, and yearly precipitation up to July 31 was 325 mm (U.S. Climate Data 2022).

Winter Storm Uri

Beginning 10 February 2021, temperatures throughout North America dipped because of a low-pressure trough from a storm system moving in from the Pacific Northwest. A second, larger trough that developed over the central United States, was aided by a polar vortex that pulled much colder temperatures into the southern United States and northern Mexico on 13 February bringing the winter storm into the southern Texas region. Fully forming on 15 February 2021, the trough fed moisture into the winter storm, leading to a historic cold wave affecting the central and eastern United States, including Texas. Texas experienced record low temperatures from 12–20 February. Port Mansfield experienced temperatures below freezing from 18 to 20 February with the record low temperature of 7 °C occurring on 18 February. Historic normal low and high temperatures from 12–20 February from 1981 to 2010 ranged from 11.7–12.3 °C for lows and 20.8–21.2 °C for highs (U.S. Climate Data 2022).

Methods

Our study site was the 11,330 ha El Sauz ranch in Willacy and Kenedy Counties, Texas, in the Gulf Coast Prairies and Marshes ecoregion (Gould et al. 1960). The ranch, owned and managed by the East Foundation for ranching, science, and educational purposes, is located on the coast of the Gulf of Mexico (Fig. 1), and vegetation directly adjacent to the coast is dominated by Gulf cordgrass (*Spartina spartinae*). Gulf cordgrass is a native bunchgrass that dominates large areas of coastal rangelands (Haynes et al. 2018). Inland from the Gulf cordgrass is a mixed grass community that is dominated by seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), Gulfdune paspalum (*Paspalum monostachyum*), and a greater diversity of herbaceous plants than occurs in the Gulf cordgrass community. Average annual high temperature at Port Mansfield, Texas, from 1981 to 2010 was 26.7 °C; annual low temperature was 18.9 °C (U.S. Climate Data 2022).

Our study used sixteen units ranging from 200 to 485 ha that were part of a prescribed burning study. Fire regimes consisted of season of burning (winter burn, summer burn, no burn) and return interval (long or short) and were

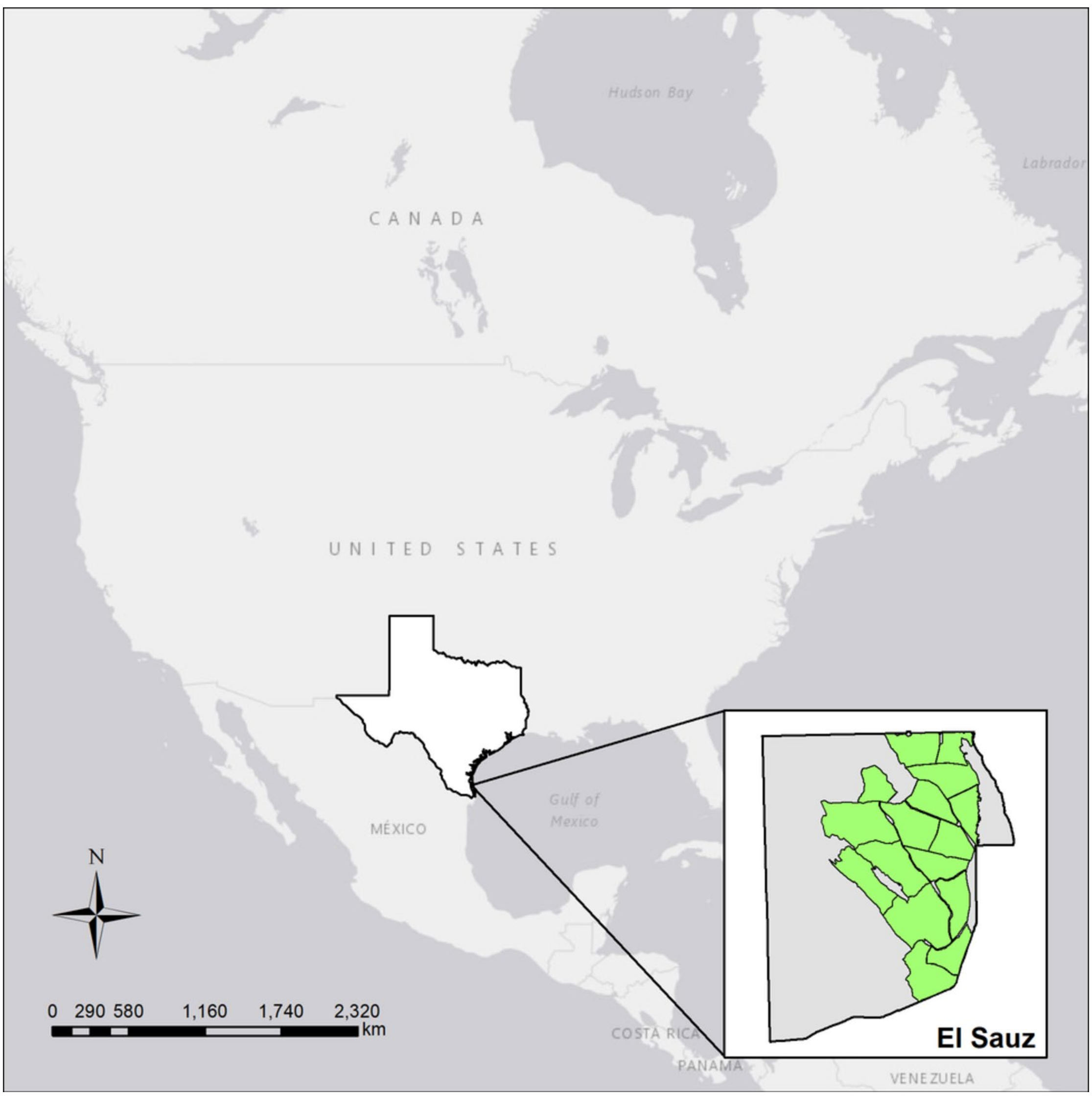

Fig. 1 Location of East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA

randomly assigned to units. This resulted in 3 × Winter Short interval (WS), Summer Short interval (SS), Summer Long interval (SL), and Control units (C), and 4 × Winter Long interval units (WL) (Fig. 2). Summer burn units were burned during July or August; winter burns took place during January or February. Short return interval units were burned every 3 years, while long return interval units were burned every 5 years. The initial prescribed burning treatments began in 2016. Burn units received repeated treatments according to their assigned fire regime (season and return interval) (Table 1).

Four 100 × 10 m belt transects were placed near the center of each study unit to form a square array. Units near the coast had areas dominated by Gulf cordgrass and areas that include other herbaceous communities, typically dominated by seacoast bluestem. In those units a sampling array was placed in both the Gulf cordgrass-dominated vegetation communities and mixed grass vegetation (non-Gulf cordgrass, Fig. 3). Units located further inland did not have any Gulf cordgrass; thus, they had one sampling array placed within the mixed grass community. Sampling arrays were placed as close the center of the unit, or the center of the vegetation community as possible. There were 24 sampling arrays totaling 96 transects in our study area, with $n = 16$ transects in WL, and $n = 20$ transects each in C, WS, SL, and SS.

We conducted monthly walking butterfly surveys from March 2020 through February 2022 for all sampling arrays using a slightly modified Pollard method (Pollard 1977). Three months during the second year of the study, July, August, and September 2021, we were not able to sample several units because of standing water. As a result, we did not include those three months in any of our analyses. We conducted surveys between the hours of 0900 to 1600 (fall-spring) and 0800 to 1700 (summer). Surveys were only conducted when air temperature was above 17 °C and there was no precipitation. Time, temperature, windspeed, and cloud cover were recorded at the beginning and end of each butterfly survey. Cloud cover was recorded as < 25%, 25–50%, 50–75%, or > 75%. Ideal wind conditions were below 4.5 m/s and ideal cloud cover was below 50% coverage; however, ideal cloud cover conditions could not always be met.

We walked transects at a pace of approximately 5 min per 100 m. All adult butterflies observed within each 100 × 10

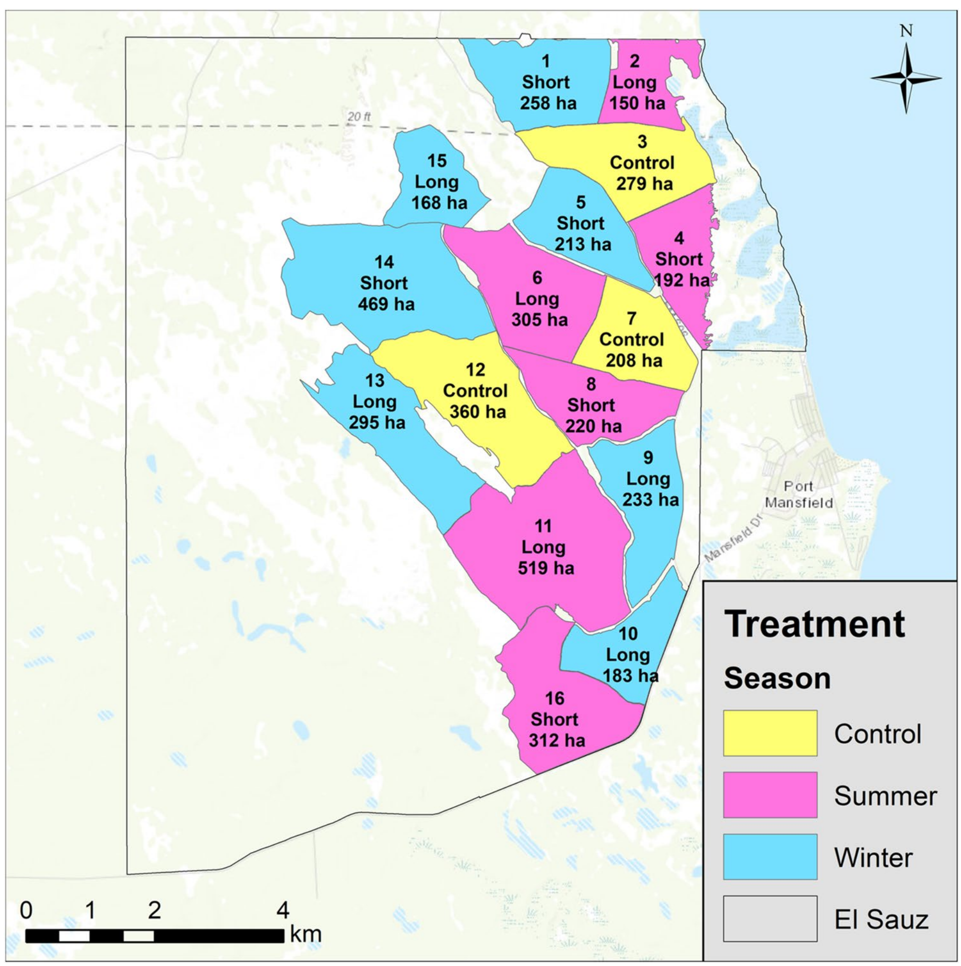

Fig. 2 Burning treatment and unit size for study of prescribed fire effects on butterfly populations, 2020–2022, at East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. Blue = Winter burn; Purple = Summer burn; Yellow = Control. Summer = July or August; Winter = January or February. Short fire return interval = 3 years; long fire return interval = 5 years

Table 1 Fire regime and size of units for butterfly population study at East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, 2020–2022

Unit ID #	Area Ha (Ac)	Season of burn	Return interval	Initial burn (Mo-Yr)	Second burn (Mo-Yr)	Fire regime
1	258 (639)	Winter	Short	Feb-17	Feb-20	WL
2	150 (371)	Summer	Long	Jul-16	Aug-21	SL
3	279 (690)	Control	NA	NA	NA	C
4	192 (474)	Summer	Short	Aug-17	Jul-20	SS
5	213 (525)	Winter	Short	Feb-17	Feb-20	WS
6	305 (753)	Summer	Long	Jul-16	NA	SL
7	208 (514)	Control	NA	NA	NA	C
8	220 (543)	Summer	Short	Aug-17	Aug-20	SS
9	233 (577)	Winter	Long	Feb-16	Feb-21	WL
10	183 (451)	Winter	Long	Feb-16	Feb-21	WL
11	519 (1282)	Summer	Long	Sep-19	NA	SL
12	360 (889)	Control	NA	NA	NA	C
13	295 (729)	Winter	Long	Feb-19	NA	WL
14	469 (1160)	Winter	Short	Jan-19	Feb-22	WS
15	168 (414)	Winter	Long	Jan-19	NA	WL
16	312 (771)	Summer	Short	Sep-19	NA	SS

Winter = January or February; Summer = July or August. Short Interval = 3 years; long interval = 5 years

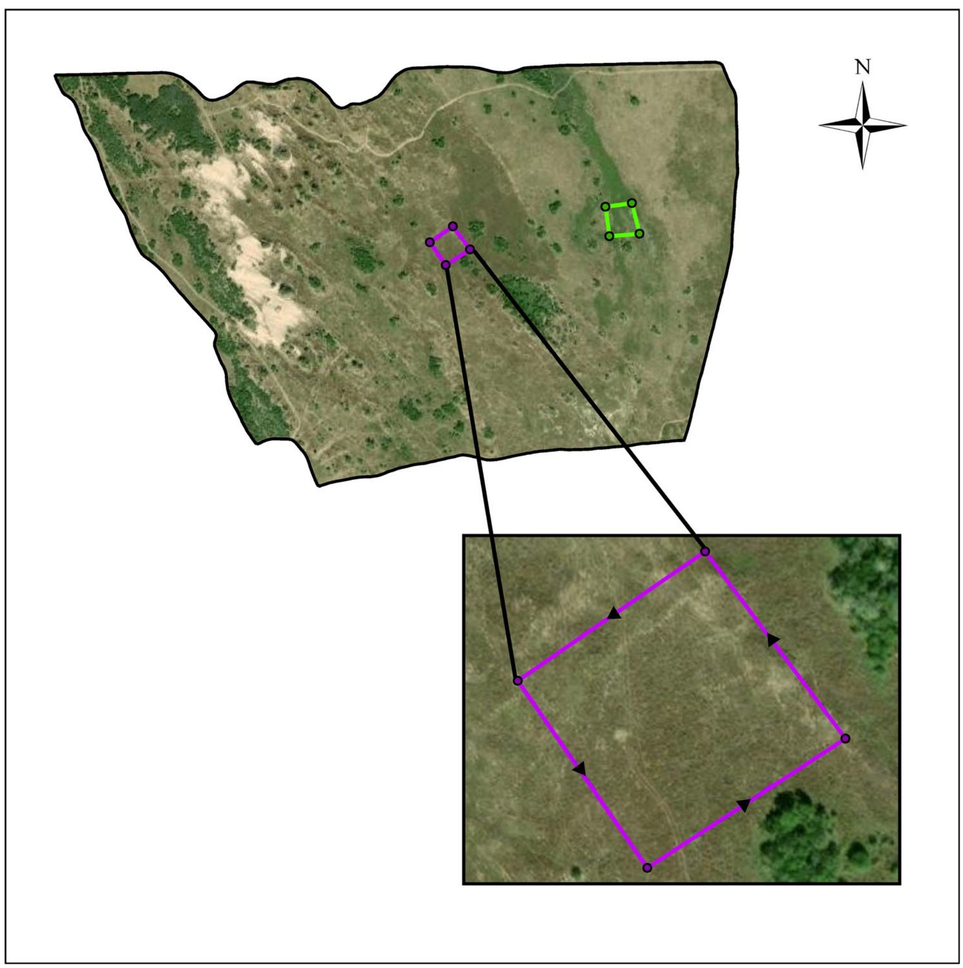

Fig. 3 Butterfly sampling arrays located within a prescribed burn unit at East Foundation's El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, 2020–2022. Green represents an array located in a Gulf cordgrass-dominated plant community. Purple is a mixed grass/non-Gulf cordgrass array. Arrays consisted of four 100 × 10-m belt transects forming 90° angles at their intersections

m belt transect were identified to species with the exception of individuals in two subfamilies. Members of the Theclinae and Polyommatinae subfamilies, in the family Lycaenidae, were identified and recorded only as "HAIR" and "BLUE" respectively, because of the difficulty of identifying them in flight. Any butterflies we weren't able to identify in flight were caught with a butterfly net, identified, and released. Surveys took on average 3 days per month. When weather conditions were met we visited approximately eight transect arrays per day. Arrays were sampled randomly, although to reduce driving time, arrays within a group were often visited within the same day: coastal arrays located on the eastern portion of the ranch, inland arrays located on the western portion of the ranch, and arrays located in between these two groups.

Statistical analysis

We compared butterfly abundance in the sampling month prior to Hurricane Hanna (July 2020) to the sampling month following the hurricane (August 2020). We limited the comparison to 1 month prior and 1 month following the event because of the ephemeral nature of butterfly populations, i.e., we would expect butterfly populations to naturally change over time in the absence of a hurricane if we used a longer period; however, there are not major seasonal changes in butterfly abundance expected between July and August in this study area. To investigate effects of Winter Storm Uri, we compared transect totals for March, April, and May 2020 (no freeze) to March, April, and May 2021 (post-freeze). Three months were compared in this analysis because there may have been lingering effects on plants over the months following days of record below-freezing temperatures.

For both analyses we used total number of butterflies per array (0.4 ha). Data were analyzed with a generalized linear mixed model with fire regime and month, as well as their interaction, as fixed effects; transect within fire regime was a random effect that was the subject for a repeated measures analysis with a first-order autoregressive, heterogeneous variance–covariance structure to account for temporal non-independence. Butterfly numbers were modeled as following a negative binomial distribution with a log link function.

When the ECE had an effect on abundance we created a hotspot map to visualize areas of high impact versus areas of low impact. We categorized each butterfly observed into its family to create family totals for each sampling array each month. We excluded 20 unidentified butterflies from the dataset. We calculated the center coordinate for each sampling array in a GIS using the Mean Center tool in ArcMaps, assigned sums of butterfly families on each array to its CenterPoint coordinate, and used a point density analysis.

We used the Topo-to-Raster tool in ArcMaps for each month using Month/Year_Family as input for the Field option and point elevation as the Type. This interpolation provided a monthly snapshot of total butterfly abundance at the different sampling arrays (hotspots) within the study site. After each month's raster had been created, we used the Raster Calculator to add designated seasons and families. Lastly, we summed March, April, and May 2021 abundance and subtracted it from the sum of March, April, May 2020 to show differences in total butterfly abundance between the 2 years.

Results

Approximately 50% of survey days met the ideal average cloud cover of less than 50% (Table 2). All other weather conditions defined earlier were met for each survey.

We recorded 4889 individual butterflies from 44 species and 2 subfamilies that were not taken to species during our study (Supplemental Table 1). This included individuals from all six butterfly families (Hesperiidae 442, Lycaenidae 1266, Nymphalidae 1560, Papilionidae 122, Pieridae 1472, Riodinidae 7) and 20 unidentified individuals.

Table 2 Monthly average weather conditions recorded during butterfly surveys at East Foundation's El Sauz ranch in Willacy and Kenedy Counties, TX, USA, 2020–2022

Month of study[a]	Calendar month	Year	Average temperature (°C)	Average wind speed (m/s)	Average cloud cover (%)
1	3	2020	27.0	2.7	> 75%
2	4	2020	31.0	2.0	> 75%
3	5	2020	30.8	3.1	50–75%
4	6	2020	32.6	2.7	25–50%
5	7	2020	35.3	2.1	25–50%
6	8	2020	34.6	2.7	25–50%
7	9	2020	30.4	2.5	25–50%
8	10	2020	29.4	3.9	25–50%
9	11	2020	29.8	1.7	25–50%
10	12	2020	24.9	1.4	50–75%
11	1	2021	19.8	2.7	25–50%
12	2	2021	23.3	2.5	> 75%
13	3	2021	23.4	2.9	50–75%
14	4	2021	26.6	2.7	> 75%
15	5	2021	28.8	2.9	50–75%
16	6	2021	31.9	2.1	25–50%
20	10	2021	32.0	1.4	25–50%
21	11	2021	26.8	2.4	< 25%
22	12	2021	23.2	1.4	> 75%
23	1	2022	16.0	1.6	> 75%
24	2	2022	21.9	1.8	50–75%

[a]Months 17–19 were excluded from our study as several units were inaccessible during those months because of standing water

Hurricane Hanna

Butterfly sampling arrays were purposefully placed in units with varying fire regimes as part of a larger project, so we tested effects of the hurricane in each fire regime. Effects of Hurricane Hanna were consistent across landscape conditions (fire regimes) (Fig. 4). There was also no effect of Hurricane Hanna on total butterfly abundance at our study site ($F_{1,80} = 1.84$; $P = 0.1786$) (Fig. 5).

Winter Storm Uri

Effects of Winter Storm Uri's prolonged record cold temperatures in February 2021 on total butterfly abundance depended ($F_{4,54} = 3.44$, $P = 0.0141$) on fire regime (Fig. 6). There were fewer butterflies post-winter storm than pre-winter storm in SL ($F_{1,\,52.6} = 13.87$, $P = 0.0005$), SS ($F_{1,52.6} = 24.4$, $P < 0.0001$) and WL ($F_{1,58.6} = 24.05$, $P < 0.0001$). The winter storm had no effect ($F_{1,52.6} = 1.51$, $P = 0.2248$) on butterfly abundance in the control or WS fire regimes ($F_{1,52.6} = 1.17$, $P = 0.2844$); however, these fire regimes also had the lowest pre-freeze abundance as well.

Visually, it is difficult to discern clear trends in abundance change on the hotspot map showing the differences between March through May 2020 (before Winter Storm Uri), and March through May 2021 (following Winter Storm Uri) (Fig. 7). On the hotspot map the "hotter" colors (yellows) indicate the greatest differences between the 2 years, and the "cooler" colors (blues) indicate less difference between the years. There was no fire regime that consistently showed either cooler or hotter colors. Cooler colors (indicating the least difference) tended to be found more often in control and winter burn units, although not all control and winter burn units displayed cooler colors. Hotter colors, where the differences between 2020 and 2021 were greatest, were most often found in units along the east side of the study site, closest to the Gulf of Mexico.

Discussion

Extreme weather events (sensu IPCC 2023) are not only more frequent and intense as a consequence of climate change (Ummenhofer and Meehl 2017) but also are, by definition, difficult to predict at the local scale (Bailey and van Pol 2016). Coupled with the lack of long-term monitoring data on many plant and animal populations (e.g., Lindenmayer et al. 2022), it is unlikely that historical data can be

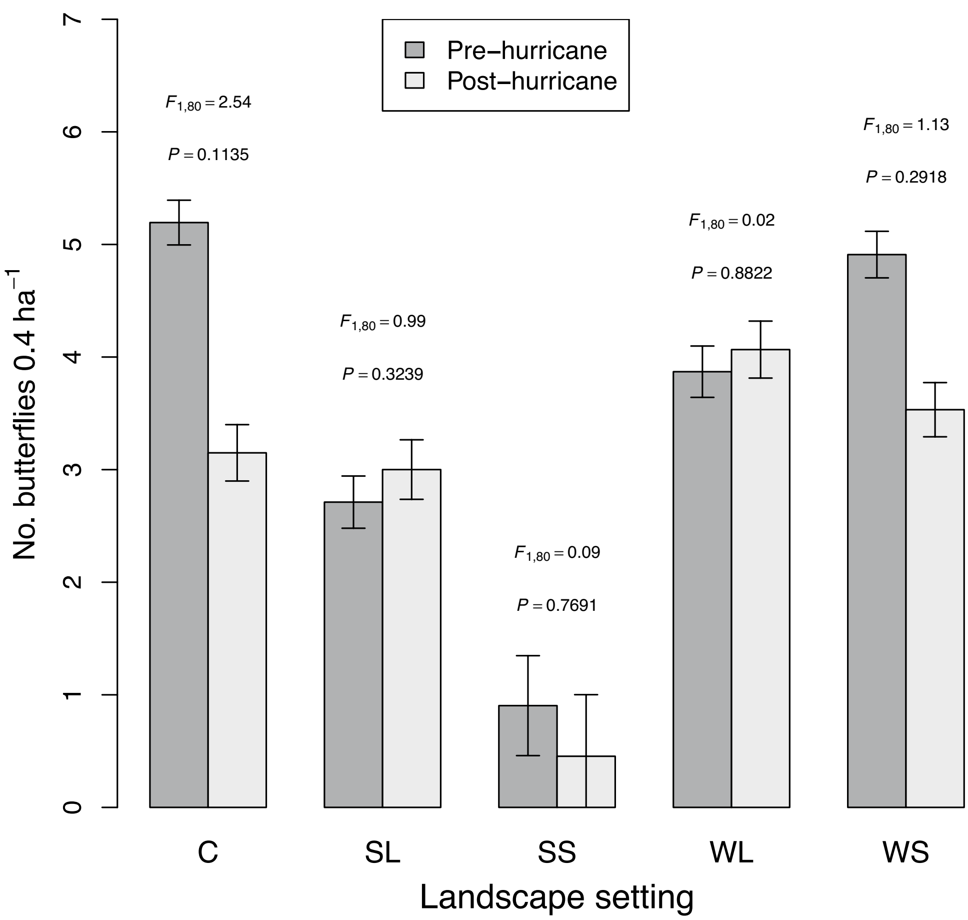

Fig. 4 Butterfly abundance at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, pre and post Hurricane Hanna, July 2020, across burn treatments. Pre-hurricane data were collected in July 2020, and post-hurricane data were collected in August 2020. C = Control; SL = Summer burning, Long interval; SS = Summer burning, Short interval; WL = Winter burning, Long interval; WS = Winter burning, Short interval. Summer = July or August; Winter = January or February. Short interval = 3 years; Long interval = 5 years

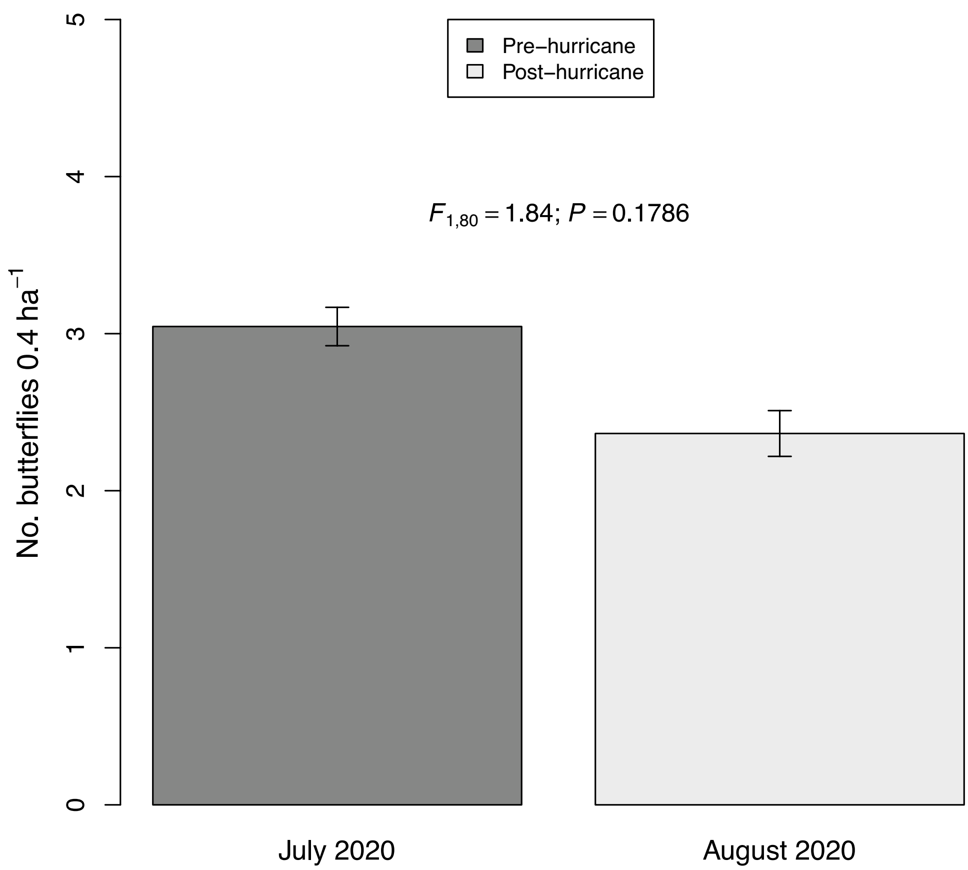

Fig. 5 Butterfly abundance at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, pre- and post-Hurricane Hanna (July 2020). Pre-hurricane data were collected in July 2020, and post-hurricane data were collected in August 2020

brought to bear when assessing effects of an extreme weather event. In our case, initiating a butterfly-monitoring study in early 2020 at permanent sampling points with monthly data collection provided a serendipitous opportunity to compare before-and-after estimates of butterfly abundance at two different temporal scales in response to two different kinds of extreme weather events. For Winter Storm Uri, we were able to compare butterfly populations 3 months post-storm to the same 3 months one year prior to the storm; and for Hurricane Hanna, we compared populations 1 month pre- and 1 month post-storm. Although we acknowledge that longer-term data prior to both events would enrich our assessment of their effects, our data (albeit somewhat limited) nevertheless add to our understanding of how butterflies respond to such events.

Precipitation can impact butterfly populations both positively and negatively, depending on butterfly species and rainfall amount (Comay et al. 2021; Munyuli 2013). We detected no response of butterfly abundance to Hurricane Hanna. Although precipitation from this one event was nearly sixfold the historic average amount for the month of July, winds were not as severe as hurricanes of greater magnitude and power. It is important to consider the increased precipitation of the hurricane in context of precipitation in the preceding months. In the three months prior to the hurricane, April–June 2020, Port Mansfield received 264.4 mm of rainfall (PRISM Time Series and Data 2022), whereas 153.2 mm is the historic average for these three months (U.S. Climate Data 2022). In a 3-year study of multispecies butterfly communities across a climatic gradient (i.e., wet, transition, and dry forests) in western Ecuador, Checa et al. (2019) found that variation in precipitation regimes might significantly affect butterfly species that display strong seasonality, such as those in our study. Long et al. (2017) determined that although extreme temperatures had greater impacts on butterfly populations, extreme precipitation, particularly wet summers, during the pupal life stage of univoltine butterfly species had detrimental effects on populations in the U.K. Because our study site was already impacted by wetter-than-normal conditions, effects of extreme rainfall during the hurricane may have been diluted.

A possible explanation for the lack of effect of Hurricane Hanna on butterfly abundance is a lack of effect on the vegetation. Our study units were located in grassland-dominated areas with few trees to be broken or damaged by high winds. Flooding in low-lying areas of the ranch was the longest lasting effect of the hurricane. Although flooding may have directly impacted butterfly eggs, larvae, and pupae (because these life stages are not as mobile as adults) adults may have been able to access refuge from rainfall, winds,

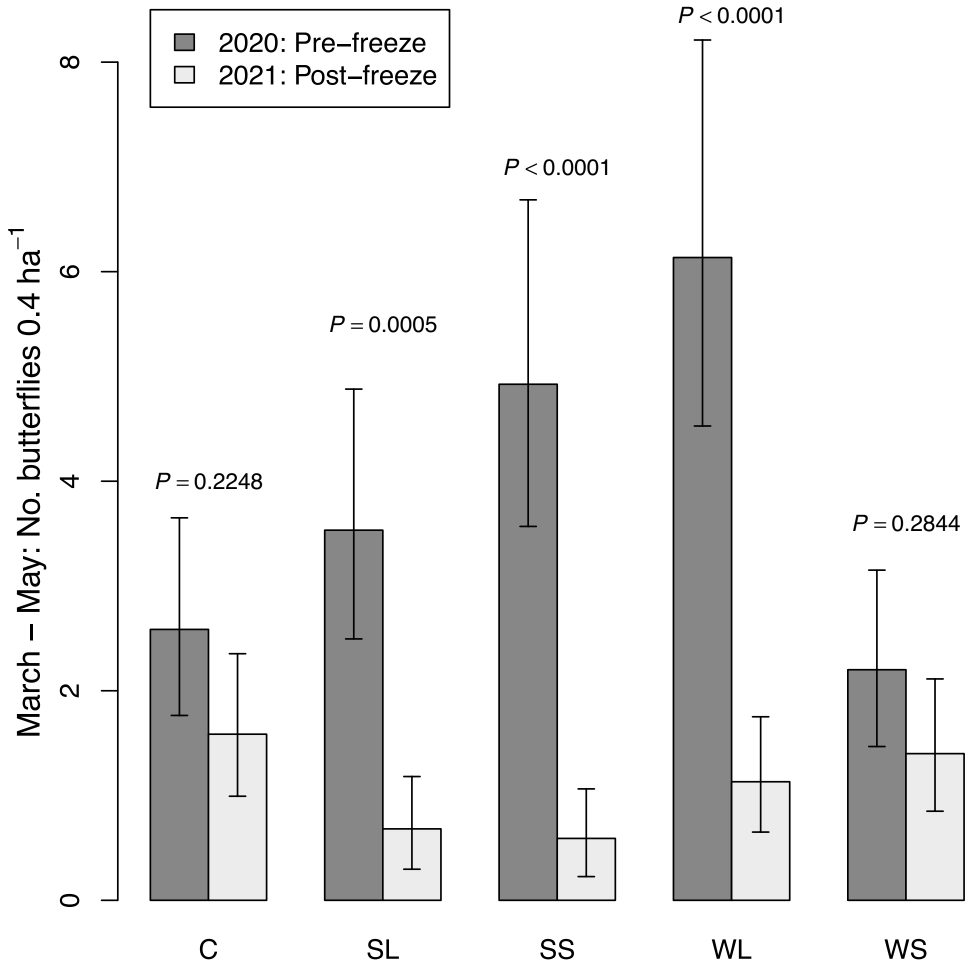

Fig. 6 Butterfly abundance relate to Winter Storm Uri in February 2021 at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA, March–May 2020 (no freeze) compared to March–May 2021 (following freeze) across prescribed burn treatments. C = Control; SL = Summer burning, Long interval; SS = Summer burning, Short interval; WL = Winter burning, Long interval; WS = Winter burning, Short interval. Summer = July or August; Winter = January or February. Short interval = 3 years; Long interval = 5 years

and flooding. Adults from nearby non-flooded areas may have repopulated and/or recolonized flooded areas shortly after flooding subsided.

Additionally, increased rainfall may assist butterflies in the long term. Vegetation productivity would have been enhanced with ample soil moisture late in the summer, as was documented after Hurricane Harvey in 2017 (Ries et al. 2018). This increase in vegetation biomass could lead to more host plant availability for butterflies. Because herbaceous plants were not destroyed by the hurricane, it is unlikely that there would have been indirect effects on butterfly populations from damage to the habitat immediately following the hurricane. Comay et al. (2021) reported a positive correlation between precipitation and overall abundance of two butterfly species in a study examining environmental controls on butterflies in Israel. In our study, 826 butterflies were recorded on the ranch in October 2020, approximately 2 months after the hurricane. This count, the highest of any month in our 24-month study, may have been a result of precipitation received from the hurricane in late July creating a surge of herbaceous growth. However, increases in butterfly populations have also been documented during and following extreme drought. De Palma et al. (2016) documented significant increases in abundance of butterflies, accompanied by changes in community composition, during an extreme drought in 1995, and populations had not returned to normal by the following year. They also noted that heterogeneity in surrounding landscapes mediated community responses to the drought. It is possible that the varied prescribed fire regimes, of winter and summer burning with either long or short interval that began in 2016 at our study site, and the resulting time-since-burning variation in vegetation mediated responses to extreme rainfall at our site.

Extreme cold weather can have both direct and indirect impacts on butterflies. A direct impact on butterflies is death of individuals in various life stages, such as Calvert et al. (1983) documented in overwintering adult monarch butterflies. In March, April, and May 2020 combined, we recorded 500 butterflies across all fire regimes. This is compared to only 146 butterflies recorded during the same months in 2021 immediately following Winter Storm Uri. This represents a 70.8% decrease in total butterfly abundance. Individually, Summer Short, Summer Long and Winter Long interval burning units experienced significantly

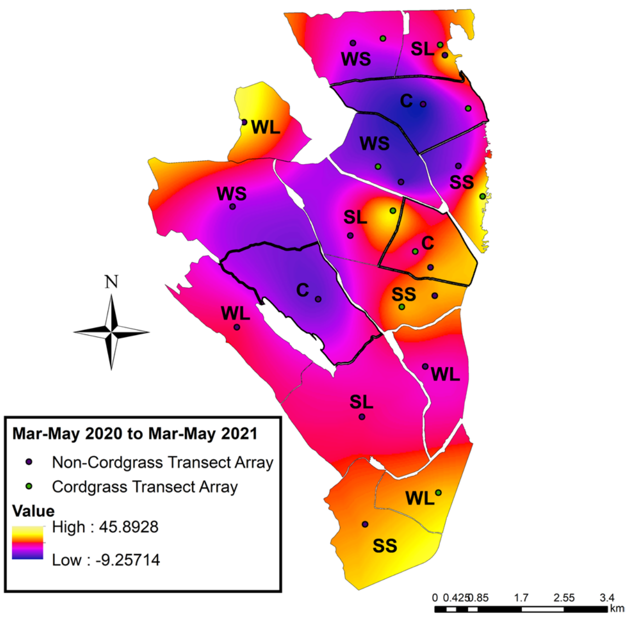

Fig. 7 Differences in butterfly abundance on sampling arrays (0.4 ha^{-1}) within prescribed fire treatments between March–May 2020 and March–May 2021 (after Winter Storm Uri in February 2021) at El Sauz Ranch in Willacy and Kenedy Counties, TX, USA. Greater differences in abundance are indicated with hotter colors (yellow), and lower differences in abundance are shown with cooler colors (blue). C = Control; SL = Summer burning, Long interval; SS = Summer burning, Short interval; WL = Winter burning, Long interval; WS = Winter burning, Short interval. Summer = July or August; Winter = January or February. Short interval = 3 years; Long interval = 5 years

lower butterfly abundance in 2021 compared to 2020. In the case of the Winter Long interval regime, two of the four units had been burned in early February 2021, approximately 10–15 days before the winter storm. However, the prescribed burning portion of our study indicated that winter burning did not have an effect on butterfly abundance (Zerlin 2022). Abundance in the Control and Winter Short interval fire regimes was not different following the winter storm in 2021 compared to 2020. Two of the three Winter Short interval units had been burned in February 2020, but we recorded no effect of burning on butterfly abundance in the months immediately following those burns either (Zerlin 2022). These results indicate that Winter Storm Uri reduced butterfly abundance in the Summer Short, Summer Long, and Winter Long fire regimes. It is likely that the freezing temperatures at our site may have contributed to butterfly mortality throughout various life stages, which is what led to a drop in butterfly abundance during the months following the freeze in three of the fire regimes. Eggs and larval stages may have been protected under an accumulation of litter in the control units in which we recorded no impact.

Indirect impacts include fire's effects on vegetation, such as host plants that butterflies use. Hallac et al. (2010) observed 50% of larval Florida Leafwing butterflies (caterpillars) dead or without a nearby food source after multiple days of freezing temperatures at Everglades National Park. The season in which burning takes place affects its outcome on herbaceous vegetation; this has been recorded in previous studies in southern Texas. Britton et al. (2010) reported a decrease in the frequency of betony-leaf mistflower (*Conoclinium betonicifolium*) one year after summer burning on Matagorda Island, Texas, whereas winter burning had no effect. Legumes, such as partridge pea (*Chamaecrista fasciculata*), hoary milkpea (*Galactia canescens*), and American snoutbean (*Rhynchosia americana*) increased 1 year after summer burning over both winter burn and control treatments. Frequency of legumes remained higher 2 years after summer burning than they were in both winter burn and control units. Thus, although it would be reasonable to expect impacts from burning during different seasons on the effects of Winter Storm Uri, our results do not show a clear trend. Although winter burning with a long interval and summer burning with both long and short intervals resulted in lower butterfly abundance than the non-burned areas, winter burning with a short interval did not.

Season of burn effects on herbaceous vegetation are not always clear. Ruthven et al. (2002) recorded that forb density increased following early winter burns and grass densities were highest after mid-winter burns on the Chaparral Wildlife Management Area in the western plains of southern Texas. Although we recorded no clear impacts of season of burn on butterfly abundance following Winter Storm Uri, we documented decreased abundance in three of the four fire regimes over the non-burned, control regime. In addition to direct impacts to butterflies from lack of protective litter, having little to no litter remaining in recently burned units also left tender vegetation in regrowth stages after burning with no protection from extreme low temperatures. Britton et al. (2010) reported that litter loads were decreased significantly both 1 and 2 years following fire in both summer and winter seasons.

Abundance of butterflies in our study was consistently lower from January through April across all our study units regardless of fire regime or year (Zerlin 2022). This somewhat limits our conclusions regarding how season of burning may have affected butterfly abundance following Winter Storm Uri. However, it is not surprising that we recorded lower butterfly abundance during those months because we also recorded some of the lowest average temperatures during our surveys in those months. Butterflies need warmer temperatures to support flying (Kral-O'Brien et al. 2021), and grassland butterflies are easier to detect when flying or nectaring (Kral-O'Brien et al. 2020).

In our interpretations of the effects of these two weather events, we acknowledge that Hurricane Hanna occurred in the interim between our pre- and post-Winter Storm Uri data. Thus, it is possible that effects of Hurricane Hanna are confounded with effects of Winter Storm Uri. In the absence of long-term data prior to our extreme weather events that would have established an “expected pattern” of butterfly population fluctuations both intra- and inter-seasonally, we acknowledge that one storm, or both storms, or an interaction between them may have affected butterfly populations above and beyond natural temporal variability.

Conclusion

With climate change comes a higher frequency of extreme climatic events, such as the hurricane and prolonged record freeze that occurred during our study (IPBES 2019; IPCC 2021). Effects of freezes in tropical to subtropical environments are likely more detrimental to butterfly abundance than low-magnitude hurricanes. Multiple disturbances within short timeframes, such as fire, floods, and freezes will have varied effects on butterfly populations that are difficult to predict. Smith (2011) indicated that more research is needed to identify how ecosystems respond to these events brought on by climate change, and our study supports this. Butterflies are important pollinators that provide valuable resources for other organisms in terrestrial ecosystems. By understanding how butterflies respond to extreme weather events, we can better know how to provide protection for them from these events. We did not detect an effect of a Category 1 hurricane on butterfly populations overall and across all prescribed fire regimes. There was a significant reduction in butterfly abundance, however, as a result of the 2021 winter storm, and its effects depended on fire regime.

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Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by RRZ and JCE. Analyses were performed by DBW, RRZ, and SR-H. The first draft of the manuscript was written by RRZ, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors have no financial interests, competing interests, or other declarations.

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