EFFECTS OF LAND USE AND MANAGEMENT PRACTICES ON GRASSLAND BUTTERFLY COMMUNITIES

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Abstract: Grassland butterflies are undergoing worldwide population declines due to habitat loss and degradation. Rangelands in the southern Great Plains; can provide habitat for grassland butterflies depending on management practices. As grasslands decline, grassland-dependent species, such as grassland butterflies, undergo widespread population losses. To manage remaining grasslands, patch-burn grazing, prescribed fire, and mowing/haying are commonly implemented management practices across the southern Great Plains. However, the impact of management on the butterfly communities is complex, and the effects of different management regimes on butterfly communities are not clear. I investigated the impact of time since prescribed fire and season of fire on butterfly communities in cattle-grazed rangelands in north-central Oklahoma. Species richness varied by time since fire and season of fire, with older spring-burned sites having the highest species richness. Diversity indices and evenness varied by treatment, with older spring-burned sites having the lowest evenness and inverse Simpson's Diversity while recently spring-burned sites had the lowest Shannon-Wiener Diversity of all treatments. Patch-burn grazing creates a mosaic of successional vegetation stages which can benefit different butterfly species and support the overall community. To untangle the effects of variable management regimens and habitat characteristics on butterfly community composition and butterfly community traits, I conducted butterfly and flowering forb surveys at sites across north-central Oklahoma. A total of 942 butterflies were recorded across 39 species over two years, with community measures differing by site. Neither land use intensity nor habitat characteristics had measurable effects on overall butterfly community composition or butterfly community traits. This research adds to the growing body of literature on butterfly community ecology and highlights the need for further studies to understand what factors drive butterfly community patterns. Finally, I created ecological niche models for five *Speyeria* species of conservation interest by combining each species' known occurrences with climate and environmental variables to identify important response variables and determine the potential distribution of suitable habitat for each species. Response variables differed among species, which highlights each species' different climate and habitat needs. This demonstrates the value of citizen science and photo sharing websites for providing important data for evaluating species distributions.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

Table Page

Table Page

LIST OF FIGURES

4.5. Ecological niche model for Aphrodite fritillaries (*Speyeria aphrodite*)..........128

4.5. Ecological niche model for Aphrodite fritillaries (*Speyeria aphrodite*)..........128

Figure Page

CHAPTER I

INTRODUCTION

Grassland butterflies have undergone population declines around the world, with multiple species in North America listed as threatened or endangered (New et al. 1995; Swengel et al. 2011). Part of this decline is due to habitat loss, particularly within grasslands (Samson and Knopf 1994; Schlicht and Orwig 1998). Native shortgrass, mixed-grass, and tallgrass prairie habitats have been lost due to land-use change including urban development and agricultural production (Samson and Knopf 1994; Wolters et al. 2000; Samson et al. 2004). Additionally, grasslands have been lost due to the removal of historic disturbance regimes including the suppression of fire and removal of free-roaming bison (Samson et al. 2004).

The vast majority of rangleands are not burned, but for those that are approaches to prescribed fire management in vary with different sizes of fire, seasons of fire, and fire return intervals (Knapp et al. 2009). One type of fire management is patch-burn grazing, which focuses on burning portions of pastures often in combination with livestock grazing (Steuter et al. 1995; Fuhlendorf and Engle 2001). The use of livestock grazing and fire creates a shifting mosaic of burned and grazed areas which increases heterogeneity within a landscape (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Churchwell et al. 2008; Holcomb et al. 2014).

A majority of grassland butterflies respond negatively to fire (Thom et al. 2015; Kral et al. 2017). However, populations can recover after fire but the amount of time before the population reaches pre-fire levels varies by species and is dependent on many factors, including the ability to recolonize from nearby unburned areas (Swengel 2000; Thom et al. 2015) and species life history traits such as voltinism (Swengel 2000; New 2014; Kral et al. 2017).

Butterfly species responses to different fire regimes (Vogel et al. 2007) may reflect fire effects on vegetation. Fire alters local vegetation communities (Huntzinger 2003), stimulates wildflower growth (Moranz et al. 2014), and alters plant phenology and growing season length (Wrobleski and Kauffman 2003; Mola and Williams 2018). Additionally, fire modifies habitat structure by creating more bare ground and shorter vegetation with less litter (Sparks et al. 2009; Henderson 2018).

Because of these diverse responses to fire, it is difficult to develop a prescribed fire regime to benefit the overall butterfly community (Schultz and Crone 1998; Vogel et al. 2007). Patch-burn grazing may therefore provide a solution by creating a mosaic of habitat patches with different times since fire. Chapter one investigates the effects of patch-burn grazing on the butterfly community with the aims to determine how time since fire and season of fire since last patch-burn influence butterfly community measures, community assemblages, and blooming plant availability.

In addition to the use of patch-burn grazing, land managers can also use fire without grazing and mowing/haying (Swengel 2001, Vogel et al. 2007). It can be challenging to make comparative studies acorss a landscape because of the variability in management regimes and different frequencies of grazing, burning, and mowing/haying within sites it can make comparative studies across a landscape challenging. To combat this challenge Blüthgen et al. (2012) developed an additive Land Use Intensity (LUI) index that allows for sites that have undergone variable management regimens to be comparable on a continuous index scale. Chapter two investigates how 1) land management in the context of Land Use Intensity, 2) site level habitat characteristics, and 3) broader landscape categorization influence butterfly community composition and butterfly community traits.

In areas with sensitive butterfly species, potential distributions of species can be used to conserve species by locating areas where species exists but are not documented, identifying key areas to focus efforts on managing habitat, and estimating current distributions (Phillips et al. 2004a, Guisan et al. 2006). Potential distributions can be developed by Species Distribution Models (SDMs) (Phillips et al. 2004a). An SDM can show which environmental factors a species responds to within an environment (Miller 2010, Beane et al. 2013). This is useful for understudied species because SDMs can evaluate a species that has low occurrence records, exists in fragmented or difficult to access habitat, and needs quick assessments (Phillips et al. 2004a, Guisan et al. 2006, Miller 2010, Beane et al. 2013).

Chapter three uses ecological niche models to estimate the potential distribution of five *Speyeria* species of conservation interest east of the Mississippi River and identifies the main climate and environmental response variables for each species.

CHAPTER II

FIRE MANAGEMENT IMPACTS ON GRASSLAND BUTTERFLY COMMUNITIES IN CATTLE-GRAZED RANGELANDS

Abstract

Grassland butterflies are undergoing worldwide population declines due to habitat loss and degradation. Rangelands in the southern Great Plains, can provide habitat for grassland butterflies depending on management practices. Patch-burn grazing is a management regime that involves burning a portion of grazed pastures at different times. Livestock prefer grazing in recently burned areas resulting in low grazing intensity in less recently burned areas. The combination of patch burning and cattle grazing creates a shifting mosaic of recently burned to older burned areas and lightly grazed to heavily grazed areas. However, the impact of fire and grazing on butterfly communities is complex and the effects of different management regimes on butterfly communities are not clear. We investigated the impact of time since prescribed fire and season of fire on butterfly communities in cattle-grazed rangelands. Eight rangeland pastures, each of which contains three burn units, occur in the northern portion of The Nature Conservancy's Joseph H. William's Tallgrass Prairie Preserve. Twelve burn units were selected for inclusion in this study by availability of replicates, so the same number of units could be visited for each burn treatment. Treatments included units burned in spring 2018, summer 2018, summer 2019, and spring 2020, with three replicates of each.

Every burn unit had two standardized Pollard transects with surveys occurring three times each year. A total of 35 butterfly species were observed. Species richness varied by time since fire and season of fire, with older spring-burned sites having the highest species richness. In comparison, recently spring-burned sites had the lowest species richness. Diversity indices and evenness varied by treatment, with older spring-burned sites having the lowest evenness and inverse Simpson's Diversity while recently spring-burned sites had the lowest Shannon-Wiener Diversity of all treatments. Thirteen species were present in every treatment regardless of time since fire and season of fire while 12 species were restricted to one treatment. Additionally, time since fire and season of fire changed dominant vegetation cover, blooming forb presence, and grass hostplant dependent species presence. Patch-burn grazing creates a mosaic of successional vegetation stages which can benefit different butterfly species and support the overall community. Additionally, understanding the timing of fire in respect to butterfly species phenology can help provide context to the impacts of fire on individual species.

Keywords: butterfly community assemblages, forbs, hostplants, patch-burn grazing, prescribed fire, season of fire, time since fire

Introduction

Grassland butterflies have undergone population declines around the world, with multiple species in North America listed as threatened or endangered (New et al. 1995; Swengel et al. 2011). Part of this decline is due to habitat loss, particularly within grasslands (Samson and Knopf 1994; Schlicht and Orwig 1998). Native shortgrass, mixed-grass, and tallgrass prairie habitats have been lost due to land-use change including urban development and agricultural production (Samson and Knopf 1994; Wolters et al. 2000; Samson et al. 2004). Additionally, grasslands have been lost due to the removal of historic disturbance regimes including the suppression of fire and removal of bison (Samson et al. 2004). In the southern Great Plains, the majority of grasslands are privately owned rangelands (Reeves and Baggett 2014). Approaches to prescribed fire management in rangelands vary with different sizes of fire, seasons of fire, and fire return intervals (Knapp et al. 2009). Patch-burn grazing focuses on burning pastures in portions, rather than pastures in entirety, in order to increase spatial heterogeneity within a habitat often in combination with cattle grazing (Steuter et al. 1995; Fuhlendorf and Engle 2001). Cattle preferentially graze in recently burned areas, resulting in low grazing intensity occurring in unburned areas or areas with longer times since fire (Steuter et al. 1995; Augustine and Derner 2015). Areas that are burned and grazed shift across the landscape, creating a fluctuating mosaic of recently burned to older burned areas and lightly grazed to heavily grazed areas (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Churchwell et al. 2008; Holcomb et al. 2014).

A majority of grassland butterflies respond negatively during and immediately following a fire with an initial decline in population numbers (Thom et al. 2015; Kral et al. 2017). However, populations rebound after this initial decline, although the amount of time before the population reaches pre-fire levels varies by species and is dependent on many factors, including the ability to recolonize from nearby unburned areas (Swengel 2000; Thom et al. 2015). Direct mortality can result from fire, depending on the timing relative to the presence of different life stages (Swengel 2000). Butterfly eggs and larvae are more susceptible to mortality from fire than adults due to a lack of mobility (Swengel 2000; New 2014; Kral et al. 2017). Exposure to fire during immature stages may be more damaging to a univoltine species than a multivoltine species due to non-overlapping life stages (Brown et al. 2016). Additionally, multivoltine species have more time to recover post-fire than univoltine species due to the occurence of more generations (Swengel 1996).

Butterfly species responses to different fire regimes (Vogel et al. 2007) may reflect fire effects on vegetation. Butterflies rely on host plants for larvae and nectaring plants for adults. Fire alters local vegetation communities, with different plant species being more or less tolerant to fire (Huntzinger 2003), and stimulates wildflower growth (Moranz et al. 2014). Fire can alter plant phenology and growing season length (Wrobleski and Kauffman 2003; Mola and Williams 2018). Additionally, fire modifies habitat structure by creating more bare ground and shorter vegetation with less litter (Sparks et al. 2009; Henderson 2018).

Because of these diverse responses to fire it is difficult to develop a prescribed fire regime to benefit the overall butterfly community (Schultz and Crone 1998; Vogel et al. 2007). Patch-burn grazing may provide a solution by creating a mosaic of habitat patches with different times since fire. The aims of this study are to determine how time since fire and season of fire since last patch-burn influence butterfly community measures, community assemblages, and blooming plant availability. Identifying how patch-burn grazing regimes impact butterfly communities can provide information to land managers who want to consider butterflies when planning prescribed fire treatments.

Methods

Study site

The Joseph H. Williams Tallgrass Prairie Preserve is the largest protected tallgrass prairie in North America and is located in Osage County in northern Oklahoma (Hamilton 2007). The preserve consists of a mix of tallgrass prairie and oak woodland with grasslands being dominant and over 700 flora species recorded (Hamilton 2007; Palmer 2007). The preserve has high butterfly species richness with 96 species records, including vulnerable butterfly species like the regal fritillary (*Speyeria idalia* Drury) and the Diana fritillary (*S. diana* Cramer; Fisher 2018). The preserve is managed using patch-burn grazing with cattle and bison (Hamilton 2007; McGlinn 2009). Randomly placed prescribed fires are conducted across the preserve to create an average fire return interval of three years (Hamilton 2007). This study took place in the northern portion of the preserve in the cattle-grazed pastures, where cattle are grazed throughout the growing season (April 15- September 30) with an average stocking rate of 2.24 Ha/Head (Fig. 1). This part of the preserve has eight pastures, each of which contains three burn units. Twelve burn units were selected for inclusion in this study by availability of replicates, so the same number of units could be visited for each treatment. Units were burned in spring 2018, summer 2018, summer 2019, and spring 2020, with three replicates of each (Table 1, Fig. 1). To compare effects of time since fire, treatments were grouped into three fire classes: Recent = <1 year since fire, Intermediate = 1-2 years since fire, and Older = >2 years since fire (Adedoja et al. 2019; Table 1). There were no older summer-burned sites due to a lack of replicates available.

Field observations - butterfly community

In the summers of 2019 and 2020, two 200-meter transects for Pollard walks were placed in each of the burn units for a total of 24 transects (4 burn treatments * 3 replicates * 2 transects = 24) (Fig. 1). A Pollard transect (also known as a Pollard walk) is a standardized butterfly survey with a fixed route walked regularly at a slow pace (Pollard 1977; Pellet et al. 2012). Pollard walks were modified to count all butterflies that occurred to the sides and ahead of the observer (Swengel and Swengel 1999). Modified Pollard transects were walked three times between 0900 to 1600 hours Central Daylight Time, including an early summer survey, mid-summer survey, and late-summer survey. Each transect's starting point was randomly placed using ESRI ArcMAP 10.6.1. An additional random point was used to determine orientation of each transect. There was a buffer of at least 250 meters between transects to prevent counting the same individual more than once. In addition, transects were placed at least 100 meters from gravel roads to avoid edge effects but within 200 meters of an access point to minimize logistical constraints (Conradt et al. 2000; Reeder et al. 2005).

Prior to every survey, wind speed and temperature were recorded using a handheld Kestrel (Nielsen-Kellerman Company, PA). Transects were walked when temperature was above 13 °C and sunny (estimated cloud cover $\leq$ 30%) or if temperatures passed 17 °C regardless of cloud cover (Pollard 1977; Pollard and Yates

1993; Campbell et al. 2007; Pellet et al. 2012). Transects were only walked if wind speeds were below 16 km/h (Moranz et al. 2012). Butterfly species and counts were recorded for all individuals. All butterflies that occurred within 180° of the observer were counted with care taken to avoid double counting individuals (Swengel and Swengel 1999).

For every butterfly observed, behavior was recorded in one of seven categories: flying, nectaring, resting/basking, courtship flights/mating, mudpuddling, ovipositing, or dead, to determine if there were any differences in time since fire and season of fire on habitat utilization. If multiple behaviors were observed from one butterfly, such as flying to a flower and then nectaring, the behavior that occupied the majority of the observed time was recorded. To distinguish between resting on flowers or nectaring, only butterflies with extended proboscises were counted as nectaring individuals. Similarly, to distinguish between basking or mudpuddling, only individuals with extended proboscises were counted as mudpuddling individuals.

Field observations - site characteristics

Vegetation surveys were conducted along each transect after each modified Pollard walk. Along every transect a 1x1-m quadrat was placed in 10-m intervals, and overall cover data were estimated and assigned a category using a modified Daubenmire cover class system (1 = <5%, 2 = 5-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, 6 = >95%) to determine bare ground, litter, total forb, grass, blooming forb, non-blooming forb, and woody cover (Daubenmire 1959). Additionally, within every quadrat total flowering plant counts and species were recorded. Finally, overall vegetation height was recorded every 20 meters along the transect with the tallest height of vegetation touching the ruler recorded (Heady 1957).

Analysis

Butterfly community

Correspondence analysis (CA) ordination was chosen to evaluate patterns in butterfly composition and to compare community assemblages (Balmer and Erhardt 2001; Nelson and Nelson 2001) using CANOCO 5 (Lepš and Šmilauer 2003). The first two axes of the biplot were set to explain 100% of the variation. Infrequently-observed species (≤0.5% total butterflies counted within a fire treatment) were removed as rarely observed species add little additional data to biplots (Balmer and Erhardt 2001; Nelson and Nelson 2001; McCune and Grace 2002; Lee et al. 2015). A time since fire biplot and a season of fire and time since fire biplot were constructed to evaluate community composition similarities and differences among treatments. Butterfly species closer to a treatment in a biplot are more abundant at that treatment, while treatments close to one another have more similar butterfly communities (Vogel et al. 2007). To evaluate differences in the butterfly community by season of fire, a paired two-tailed t-test was run in R (R Core Team 2020).

We calculated diversity, evenness, and richness to represent the observed butterfly and plant communities to explain differences within the ordination biplot. Shannon-Wiener Index were calculated for each time since fire and season of fire at the burn unit level (Morris et al. 2014). The Shannon-Wiener Index (H') is most useful when data consist of both rare and abundant species (Morris et al. 2014). Species richness (S) in comparison emphasizes rare species (Morris et al. 2014). The equation H’/ln S was used to calculate Pielou’s evenness of the species distribution in each burn unit (J’) (Vandermeer 1981; Collinge et al. 2003). All community measures were calculated in R package Vegan (R Core Team 2020, version 3.3.2). Additionally, we ran linear mixed models with restricted maximum likelihood ratio test comparisons in R to determine the effect of time since fire and season of fire on butterfly species community measures and butterfly abundances (R Core Team 2020, version 3.3.2, package: lme4). We used ANOVAs to determine any differences in behavior between time since fire and season of fire.

Blooming forb community

To determine patterns of blooming forb composition among treatments, biplots were constructed using CA ordination in CANOCO, with the first two axes designed to explain 100% of the variation (Lepš and Šmilauer 2003). Similar to butterfly community analysis, two ordination biplots were created one of time since fire and one with both season of and time since fire. Biplots were used to examine patterns in the blooming forb community among treatments. Differences in blooming forb composition were determined using Shannon-Wiener Index, species richness, and Pielou’s evenness using package Vegan in R (R Core Team 2020). To compare effects of time since fire and season of fire on average total stems of blooming forb (per hectare) and plant species richness, linear mixed models with restricted maximum likelihood ratio test comparisons were run in package lme4 in R (R Core Team 2020, version 3.3.2).

Results

Butterfly community

A total of 409 butterflies and 31 species were recorded in 2019 and 500 butterflies and 23 species in 2020, for a total of 909 butterflies and 35 species across both years (total 28.8 km walked; Table 2). Four butterflies in 2019 could not be identified to species (Table 2). The time since fire butterfly community CA ordination diagram had 60.94% variance explained in the first axis (eigenvalue 0.198) for a total of 100% in the first two axes (Axis II eigenvalue 0.127; Fig. 2). Recently burned sites were along the negative portions of axis I and axis II of the biplot while intermediate burned sites were along the negative portion of axis I and the positive portion of axis II (Fig. 2). Older burned sites were found along the positive portion of axis I and the center portion of axis II (Fig. 2). Pieridae were split among the more recently burned sites and the older burned sites with *Phoebis sennae* (L.) found in older burned sites while both *E. nicippe* (Cramer) and *Zerene cesonia* (Stoll) were found in the most recently burned sites (Fig. 3). Disturbance tolerant species such as *Danaus plexippus* (L.), *Junonia coenia* (Hübner), *Colias eurytheme* (Boisduval), *C. philodice* (Godart), and *Eurema lisa* (Boisduval & LeConte) were in the center of the biplot, suggesting even occurrence across all time since fire classes (Fig. 2). The butterfly community was similar between spring burns and summer burns ($t(36) = -0.550$, p = 0.586).

The time since fire and season of fire butterfly community CA ordination diagram had 38.72% variance explained in the first axis (eigenvalue 0.204) for a total of 69.33% with the second axis (eigenvalue 0.161). Similar to the time since fire biplot, recently burned sites were found along the negative portion of axis I and older fires along the positive portion (Fig. 3). In comparison, intermediate burned sites and recently spring-burned sites fell along the positive portion of axis II (Fig. 3). Generalist species such as *Euptoieta claudia* (Cramer), *E. lisa*, *E. nicippe*, *Atalopedes campestris* (Boisduval), and *J. coenia* were more often found in the recently burned sites while habitat specialists such as the *C. pegala* were more often found in summer intermediate burned sites.

Butterfly species richness was similar across treatments (LMM: $X^2(4) = 4.97$, $p = 0.29$), with recently spring-burned sites having the lowest species richness (N = 10) and older spring-burned sites having the highest species richness (N = 21; Table 3). Butterfly species abundance was similar across treatments (LMM: $X^2(4) = 9.03$, $p = 0.07$), with recently spring-burned sites having the lowest butterfly abundance (N = 71) and recently summer-burned sites having the highest butterfly abundance (N = 309; Table 3).

Sites with the highest species diversity were recently summer-burned (1/D =6.781) and intermediate spring-burned (H' = 2.314; Table 3). Older spring-burned sites (1/D = 4.036) and recently spring-burned sites (H' = 1.939) had the lowest diversity indices (Table 3). Older spring-burned sites had the lowest evenness index (J' = 0.654) compared to sites that had recent spring-burns (J' = 0.842; Table 3).

Different butterfly species were observed at different times during the three survey periods (Table 4). Three species were only observed in early summer, two species only in mid-summer, and seven species only in late summer (Table 4). *Polites themistocles* (Latreille) and *Eurema nicippe* (Cramer) were the only species observed in early summer and late summer, but not in mid-summer (Table 4). Thirteen species were observed during all three survey periods.

While flying was the most frequently observed behavior overall (61.85-71.07%), by mid-summer nectaring (23.49%) and resting (10.04%) became more commonly observed behaviors (Table 5). By late summer, resting (16.13%) was observed more often than nectaring (11.29%; Table 5). The most common butterfly species observed nectaring were *Cupido comyntas* (Godat), *Cercyonis pegala* (Fabricius), and *Strymon melinus* (Hübner). In 2019, the most commonly observed flowering plants with butterfly nectaring behavior were *Asclepias tuberosa* (L.) (40.59%), followed by *Monarda citriodora* (Cerv. ex Lag) (17.82%) and *Vernonia baldwinii* (Torr.) (9.90%). In 2020, the most commonly observed flowering plants with butterfly nectaring behavior were *M. fistulosa* (L.) (23.08%), *M. citriodora* (12.31%), and *V. baldwinii* (12.31%). There were no differences in behaviors observed by time since fire or season of fire (ANOVA, all $p > 0.05$).

Blooming forb community

Thirty-nine blooming forb species were observed in 2019 and 2020. The time since fire blooming forb community CA ordination diagram had 59.20% variance explained in the first axis (eigenvalue 0.199) for a total of 100% in the first two axes (Axis II eigenvalue 0.137; Fig. 5). More recently burned sites were along the more negative portion of axis I and axis II of the biplot while older burns were found along the more positive portion of axis II (Fig. 5). For the time since fire and season of fire blooming forb community CA ordination, the first two axes cumulatively explained 59.94% variation with the majority coming from the first axis (33.84%; eigenvalue:

0.245; Fig. 6). Recently summer-burned treatments and older spring-burned treatments were more similar to each other than to other treatments (Fig. 6).

Flowering species richness was similar across treatments (LMM: $X^2(4) = 8.74$, p = 0.07), with older spring-burned sites having the highest species richness (N = 30; Table 6). Sites that had been recently summer-burned had the highest diversity (1/D = 10.15; H' = 2.58), while sites that had recent spring-burns had the lowest species richness and diversity (N = 10; 1/D = 2.335; H' = 1.379; Table 6). Total stems of blooming forbs were similar across burn treatments (LMM: $X^2(4) = 4.82$ p = 0.31). *Monarda fistulosa* had the highest average stems of flowering plants at 188,666 stems per hectare in intermediate summer-burned sites (Table 7). In recently summer-burned sites and sites intermediate spring-burned, *Achillea millefolium* had the highest average stems (88,000 stems per ha and 69,333 stems per ha, respectively, Table 7). In older spring-burned sites *Rubus* spp. was dominant at 51,333 stems per ha and in recently spring-burned sites *Oxalis* spp. was dominant with 36,667 stems per ha while (Table 7).

Vegetation cover class percentages differed by burn treatment. Recently burned sites had the highest percentage of bare ground (spring: 18.33% ± 1.02; summer: 18.03% ± 0.68), older spring-burned sites had the highest percentage of litter (33.08% ± 0.69), intermediate spring-burned sites had the highest amount of forbs (33.00% ± 0.66), recently spring-burned sites had the highest amount of grasses (43.35% ± 0.93), and intermediate summer-burned sites had the highest percentages of flowering plants in bloom (4.11% ± 0.59; Fig. 4). Additionally, vegetation height varied by burn treatment with recently spring-burned sites having the shortest vegetation (49.46 ± 1.81 cm) and intermediate summer-burned sites having the tallest vegetation (73.61 ± 2.83 cm).

Discussion

Over two years, we recorded 909 butterflies with butterfly species richness varying by burn treatment with recently spring-burned sites having the lowest species richness and older spring-burned sites having the highest. Timing of fire can impact butterfly species in relation to their life stage (Swengel 2000). Species that overwinter in early immature stages, such as eggs/early instar larvae, are typically still in immature stages in spring (Scott 1986). Thus, these species may be more susceptible to mortality from spring burns due to a lack of mobility (Swengel 1996; Swengel 1998). Of the 35 species of butterflies recorded, at least 21 would be in less mobile life stages (larvae or pupae) during spring burns ,which may have led to overall lower species richness in sites that had undergone more recent spring burns (Comstock 1940; Stamp 1985; Scott 1986; Scott 2020). Six species in particular (*Euphyes vestris* (Boisduval), *Prygus communis* (Grote), *S. melinus*, *Battus philenor* (L.), *C. philodice*, and *Pieris rapae* (L.)) were present in recently summer-burned sites but not present in recently spring-burned sites. These six species would be in larval or pupal stages during spring burns which could have caused high rates of mortality (Comstock 1940; Scott 1986). Our findings are similar to Swengel and Swengel (2007) who found that one year post-fire had the lowest species richness in Iowa prairies.

Grazing may influence butterfly species richness. For example, Kruess and Tscharntke (2002) found that intensively grazed pastures in Germany reduced butterfly species richness. Wallis De Vries and Raemakers (2001) concluded for sites in the Netherlands that lowering cattle stocking rates may benefit the entirety of the butterfly community. Similarly, reduction in grazing has been found to increase overall butterfly abundance across multiple studies in Europe (Söderström et al. 2001; Ellis 2003; Franzén and Ranius 2004; Wallis De Vries et al. 2007). Certain species of butterflies, however, decrease in abundance when grazing intensity is reduced (Thomas et al. 1986; Bourn and Thomas 2002; Dolek and Geyer 2002) but for those species the majority of grazing comes from wild rabbits or domestic sheep rather than cattle. Some species in the UK do well with cattle grazing, but only at moderate intensities (Warren 1994; Lewis and Hurford 1997; Smee et al. 2011). Cattle grazing intensity is variable in patch-burn grazing systems as recently burned patches undergo more intense grazing while older burned patches undergo less intense grazing (Fuhlendorf and Engle 2001; Augustine and Derner 2015). It is important to recognize that for this study, the interactions of fire and grazing occur together and cannot be separated. Studies are needed to evaluate the effects of season, duration, and intensity of cattle grazing on the butterfly community in the southern Great Plains both separately and in combination with patch-burn grazing.

Diversity indices were highest in sites that had been recently summer-burned and intermediate spring-burned. This is in contrast to other estimates of post-fire recovery for butterflies in prairies ranging from 3-5+ years after burn (Swengel 1996; Vogel et al. 2010). However, recently burned sites are more easily recolonized by highly vagile species (Swengel 1996; Thom et al. 2015). Because patch-burn grazing involves only burning part of a pasture, species may more easily recolonize burned areas from surrounding unburned areas (Schultz and Crone 1998; Doxon et al. 2011; Larson 2014; Moranz et al. 2014). The Joseph H. Williams Tallgrass Prairie Preserve is part of the largest extant native tallgrass prairie in North America (Hamilton 2007). While landscape connectivity is specific to each species, the large amount of habitat surrounding burned and unburned areas could lead to higher recolonization rates by butterfly species (With et al. 1997; Klug et al. 2011). In comparison, sites that had been recently spring-burned and older spring-burned had the lowest diversity indices and evenness. These low diversity indices and evenness may be due to different reasons, with recently spring-burned sites low due to timing of burns in comparison to species life stages (New 2014; Kral et al. 2017) while older spring-burned sites may be low due to having gone a longer time without being burned (Thom et al. 2015). As intermediate spring-burned sites had the second highest diversity indices, this may reflect the recovery period of butterflies post-fire but before species decline again due to changes in habitat in response to loss of fire (Thom et al. 2015). As species respond to fire (Schlicht and Orwig 1990; Schultz and Crone 1998; Swengel 1998) and cattle grazing intensity (Kruess and Tscharntke 2002; Sjödin et al. 2008) differently, the mosaic of habitats created from patch-burn grazing may be an effective strategy for managing butterflies at the community level because it creates patches of varying times since fire, seasons of fire, and grazing intensities (Steuter et al. 1995; Fuhlendorf and Engle 2001; Augustine and Derner 2015) that can potentially benefit a wider range of species.

We found 13 species which were present regardless of burn treatment while 12 species were only found in one treatment. Recently and older spring-burned sites accounted for the majority of butterfly species observed with recently spring-burned sites and recently summer-burned sites each having ≥50% of the species recorded categorized as disturbance-tolerant species. Out of the 13 species found in every treatment, seven species (*C. eurytheme*, *Vanessa cardui* (L.), *D. plexippus*, *E. claudia*, *J. coenia*, *E. lisa*

(Boisduval & LeConte), and *A. campestris*) are considered disturbance-tolerant species with one species (*C. pegala*) a habitat-specialist. This follows Kwon et al. (2013) who found that disturbance-tolerant species can recolonize areas after a burn more readily than habitat-sensitive species. The remaining four species (*P. themistocles*, *Thorybes bathyllus* (Smith), *E. comyntas,* and *Phyciodes tharos* (Drury)) have either no consensus in the literature or literature was not available to determine habitat specialization.

Butterflies emerge at varying times due to phenological differences between species (Scott 1986; Swengel 1996). Some species such as the *Anatrytone logan* (W.H. Edwards) are bivoltine but were only seen during the mid-summer survey suggesting that the two adult flights either occur close to one another or that the second flight occurs in late summer/early fall (Scott 1986). Conducting mid-summer fires could therefore potentially lower overall second generation numbers of *A. logan*. However, it is important to consider the life history traits of species compared to flight seasons when determining timing of immature stages. Species such as the *Agraulis vanillae* (L.) and *E. claudia* migrate for winter, but *E. claudia* was present all summer while *A. vanillae* was only present in late summer suggesting different rates of migration return (Walker 1985; Scott 1986). Therefore, understanding when a species is not seen due to being in an immature life stage versus being absent due to migration is necessary for assessing the impact of fire on a species.

Speyeria idalia and *Erynnis horatius* (Scudder & Burgess) were only seen a few times in a single season and time since fire treatment, and are considered habitat specialists. Habitat specialists are expected to be more sensitive to fire due to often having fewer generations per year than habitat generalists and more restrictive habitat requirements (Swengel 2000; Caven et al. 2017). However, one habitat specialist, *C. pegala*, was found in every burn treatment, with abundances varying across treatments. This may be due to the high prevalence of grass cover across treatments as *C. pegala* is positively associated with vegetation height and dependent on grass species as hostplants (Scott 1986; Moranz et al. 2012). Additionally, differences in abundance may be due to differences in vegetation structure with older burned sites having taller and thicker vegetation (Wrobleski and Kauffman 2003; Moranz et al. 2012; Swengel and Swengel 2015).

Only sites that had been recently spring-burned had all five species present that depend on grasses as hostplants. Grass cover dominated the year of spring burn and this may have driven grass-dependent species presence. Alternately, fire changes grass structure composition (Swengel and Swengel 2015). Grass skippers (four of the five grass-dependent species recorded) may show a preference for composition of grass structure in recently spring-burned sites than older burned sites. Runquist (2011) found grass-hostplant dependent species decline in abundance with increasing cattle grazing. The natural cattle behavior in patch-burn sites may have benefited grass hostplant dependent species by focusing grazing on new growth and reducing the grazing pressure on areas that have gone longer without fire (Churchwell et al. 2008; Augustine and Derner 2015).

Butterfly behavior changed throughout the season, with nectaring increasing by mid-summer and resting increasing by late summer. Nutrients in nectar are important in butterfly egg production (Murphy et al. 1983; Mevi-Schütz and Erhardt 2005) and increases in nectar observations during mid-summer may be due to multivoltine species gathering energy resources for mating and laying eggs. Alternatively it may be due to increased floral availability. For species that survive winter in immature stages, late summer may be a time of energy conservation, especially for females, as preparation for the energy expensive cost of egg-laying in fall (Carlton and Nobles 1996; Wells et al. 2011).

Butterflies most commonly nectared on three plant genera: milkweeds (*Asclepias* spp.), ironweeds (*Vernonia* spp.), and bee balms (*Monarda* spp.). While further research is needed to determine if these three genera were utilized more often than expected based on abundance, Bray (1994) found milkweeds to be disproportionately used as a nectar resource by butterfly species in tallgrass prairie in eastern Nebraska with ironweeds used to a lesser extent. Butterfly behavior has not been recorded in many studies evaluating the impact of fire on butterfly communities, although Pavlik et al. (2018) found butterflies showed no nectar preference and nectared indiscriminately in post-fire habitat. Similarly, we found no differences in nectaring behavior among fire treatments or any other observed behaviors. However, total nectaring observations were low and further research is needed to evaluate the impact of fire on butterfly nectaring behavior.

Season of fire and time since fire impacted flowering forb community composition, with the flowering plant community more similar between older spring-burned sites and recently summer-burned sites compared to other treatments. Spring burns and summer burns can lead to different plant communities (Howe 1994), yet our results suggest that communities burned in different seasons may resemble one another at different intervals of time. Grazing can also influence the plant community with grazing altering vegetation structure and vegetation species richness (Kruess and Tscharntke

2002). Cattle show a preference for grazing in recently burned sites over older burned sites and this may lead to plant community differences among treatments (Churchwell et al. 2008; Allred et al. 2011; Moranz et al. 2012). Vegetation community measures differed as well, with older spring-burned sites having the highest flowering forb richness and diversity. This is in contrast to other studies that have found that more recently burned sites tend to have more nectar resource availability (Ehrenreich and Aikman 1963; Pemble et al. 1981; Vogel et al. 2010). Not all species within a genus responded similarly, with *Monarda* spp. and *Asclepias* spp. varying by treatments. This is unsurprising as plant genera may contain both disturbance-tolerant and habitat-sensitive species (Auld 1996).

Current research suggests that no one management regimen is effective for all species given their different habitat needs (Schlicht and Orwig 1990; Schultz and Crone 1998; Swengel 1998; Vogel et al. 2007). However, patch-burn grazing may be the best available alternative, as it creates a mosaic of successional vegetation stages with different times since fire and grazing (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Swengel and Swengel 2007). Additionally, understanding the timing of fire in respect to the presence of vulnerable life stages can help provide context to the impacts of fire on different species.

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Tables

Table 2.1. Four burn treatments (three replicates of each) and respective years since fire by year in the Joseph H. Williams Tallgrass Prairie Preserve (Fig. 2.1). There were no older summer-burned sites due to a lack of replicates available.

Burn units	Time since fire (years)	Time since fire category	Season of fire	Time of last burn
2019				
a, b, c	<1	Recent	Summer	September 2018
d, e, f	1	Intermediate	Spring	March 2018
g, h, i	3	Older	Spring	March 2016
j, k, l	4	Older	Spring	March 2015
2020				
a, b, c	1	Intermediate	Summer	September 2018
d, e, f	2	Intermediate	Spring	March 2018
g, h, i	<1	Recent	Spring	April 2020
j, k, l	<1	Recent	Summer	September 2019

Table 2.2. Butterfly species and abundances recorded over two summers in the Joseph H. Williams Tallgrass Prairie Preserve.

Butterfly species	Common name	2019	2020	Total
Family Hesperiidae				
Anatrytone logan	Delaware skipper	0	1	1
Atalopedes campestris	Sachem	6	10	16
Atrytone arogos	Arogos skipper	3	6	9
Erynnis funeralis	Funereal duskywing	0	2	2
Erynnis horatius	Horace's duskywing	2	0	2
Erynnis juvenalis	Juvenal's duskywing	1	0	1
Euphyes vestris	Dun skipper	1	0	1
Polites themistocles	Tawny-edged skipper	10	6	16
Pyrgus communis	Common checkered-skipper	6	2	8
Thorybes bathyllus	Southern cloudywing	19	14	33
Family Lycaenidae				
Cupido comyntas	Eastern tailed-blue	105	148	253
Echinargus isola	Reakirt's blue	7	4	11
Strymon melinus	Gray hairstreak	28	0	28
Family Nymphalidae				
Agraulis vanillae	Gulf fritillary	3	0	3
Cercyonis pegala	Common wood-nymph	81	134	215
Danaus plexippus	Monarch butterfly	17	58	75
Euptoieta claudia	Variegated fritillary	15	12	27
Junonia coenia	Common buckeye	16	21	37
Phyciodes tharos	Pearl crescent	7	21	28
Speyeria idalia	Regal fritillary	1	0	1
Vanessa atalanta	Red admiral	4	0	4
Vanessa cardui	Painted lady	2	12	14
Vanessa virginiensis	American lady	0	1	1
Family Papilionidae				
Battus philenor	Pipevine swallowtail	1	0	1
Papilio cresphontes	Giant swallowtail	2	0	2
Papilio polyxenes	Black swallowtail	1	2	3
Family Pieridae				
Colias eurytheme	Orange sulphur	22	22	44
Colias philodice	Clouded sulphur	6	0	6
Eurema lisa	Little yellow	28	12	40
Eurema nicippe	Sleepy orange	1	2	3
Nathalis iole	Dainty sulphur	2	0	2
Phoebis sennae	Cloudless sulphur	2	3	5
Pieris rapae	Cabbage white	2	0	2
Pontia protodice	Checkered white	4	5	9
Zerene cesonia	Southern dogface	0	2	2
Unknown butterfly		4	0	4

Total species	31	23	35
Total butterflies	409	500	909

Table 2.3. Butterfly community measures across four burn treatments over three sampling periods during two years in the Joseph H. Williams Tallgrass Prairie Preserve.

Treatment	**Total transects (N)**	**Species richness (N)**	**Abundance (N)**	**Inverse Simpson's Index of Diversity (1/D)**	**Shannon-Wiener Index (H')**	**Pielou's Evenness index (J')**
Year						
2019	24	31	405	7.753	2.555	0.744
2020	24	23	505	5.500	2.171	0.692
Season of fire (SOF)						
Spring	30	26	434	5.321	2.294	0.704
Summer	18	20	475	6.504	2.277	0.760
Time since fire (TSF)						
Recent	12	21	380	6.667	2.335	0.767
Intermediate	24	21	325	6.085	2.256	0.741
Older	12	21	204	4.036	1.990	0.654
SOF & TSF						
Spring recent	6	10	71	4.971	1.939	0.842
Spring intermediate	6	19	159	6.515	2.314	0.786
Spring older	12	21	204	4.036	1.990	0.654
Summer recent	12	18	309	6.781	2.303	0.797
Summer intermediate	12	14	166	5.243	2.001	0.758

Table 2.4. Butterfly species recorded during three survey periods in the Joseph H. Williams Tallgrass Prairie Preserve. Color indicates percentage of total individuals observed during that time period (white = 0%, light gray ≤ 33%, dark gray = 34-66%, black = ≥ 67%).

Butterfly species	**Common names**	**Early summer**	**Mid summer**	**Late summer**
Family Hesperiidae				
Anatrytone logan	Delaware skipper	□	■	□
Atalopedes campestris	Sachem	□	▓	▓
Atrytone arogos	Arogos skipper	░	░	▓
Erynnis horatius	Horace's duskywing	□	□	■
Erynnis funeralis	Funereal duskywing	□	▓	▓
Erynnis juvenalis	Juvenal's duskywing	□	□	■
Euphyes vestris	Dun skipper	□	□	■
Polites themistocles	Tawny-edged skipper	░	□	■
Pyrgus communis	Common checkered-skipper	░	▓	░
Thorybes bathyllus	Southern cloudywing	▓	░	░
Family Lycaenidae				
Cupido comyntas	Eastern tailed-blue	░	▓	▓
Echinargus isola	Reakirt's blue	▓	▓	░
Strymon melinus	Gray hairstreak	□	■	░
Family Nymphalidae				
Agraulis vanillae	Gulf fritillary	□	□	■
Cercyonis pegala	Common wood-nymph	□	■	░
Danaus plexippus	Monarch butterfly	▓	░	▓
Euptoieta claudia	Variegated fritillary	▓	░	░
Junonia coenia	Common buckeye	░	▓	░
Phyciodes tharos	Pearl crescent	░	▓	▓
Speyeria idalia	Regal fritillary	□	■	□
Vanessa atalanta	Red admiral	□	□	■
Vanessa cardui	Painted lady	▓	░	▓
Vanessa virginiensis	American lady	■	□	□
Family Papilionidae				
Battus philenor	Pipevine swallowtail	□	□	■
Papilio cresphontes	Giant swallowtail	□	▓	▓
Papilio polyxenes	Black swallowtail	□	■	░
Family Pieridae				
Colias eurytheme	Orange sulphur	▓	▓	░
Colias philodice	Clouded sulphur	■	░	□
Eurema lisa	Little yellow	░	▓	▓
Eurema nicippe	Sleepy orange	░	□	■
Nathalis iole	Dainty sulphur	□	□	■
Phoebis sennae	Cloudless sulphur	□	▓	▓
Pieris rapae	Cabbage white	■	□	□
Pontia protodice	Checkered white	▓	░	░
Zerene cesonia	Southern dogface	■	□	□

Table 2.5. Butterfly behavior observations in the Joseph H. Williams Tallgrass Prairie Preserve across three sampling periods in summers of 2019 and 2020. Resting includes both resting and basking behaviors. Courtship includes both courtship flights and mating behaviors. Percentages and sample sizes are presented as % (N) by year and overall. Four unknown butterflies were excluded from analysis.

Behavior	**Early summer**			**Mid-summer**			**Late summer**		
	2019	2020	Total	2019	2020	Total	2019	2020	Total
Flying	74.67 (56)	67.86 (57)	71.07 (113)	52.80 (132)	70.97 (176)	61.85 (308)	50.00 (40)	69.64 (117)	63.31 (157)
Nectaring	10.67 (8)	9.52 (8)	10.06 (16)	31.60 (79)	15.32 (38)	23.49 (117)	12.50 (10)	10.71 (18)	11.29 (28)
Resting	8.00 (6)	14.29 (12)	11.32 (18)	12.80 (32)	7.26 (18)	10.04 (50)	21.25 (17)	13.70 (23)	16.13 (40)
Courtship	5.33 (4)	5.95 (5)	5.66 (9)	2.40 (6)	5.65 (14)	4.02 (20)	6.25 (5)	5.95 (10)	6.05 (15)
Mud-puddling	0.00 (0)	1.19 (1)	0.63 (1)	0.00 (0)	0.00 (0)	0.00 (0)	8.75 (7)	0.00 (0)	2.82 (7)
Ovipositing	1.33 (1)	1.19 (1)	1.26 (2)	0.40 (1)	0.40 (1)	0.40 (2)	0.00 (0)	0.00 (0)	0.00 (0)
Dead	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.40 (1)	0.20 (1)	1.25 (1)	0.00 (0)	0.40 (1)

Table 2.6. Flowering forb community measures across four burn treatments over three sampling periods during two years in the Joseph H. Williams Tallgrass Prairie Preserve.

Treatment	Total transects (N)	Species richness (N)	Inverse Simpson's Index of Diversity (1/D)	Shannon-Wiener Index (H')	Pielou's Evenness index (J')
Year					
2019	24	34	11.636	2.708	0.768
2020	24	26	8.444	2.511	0.771
Season of fire (SOF)					
Summer	18	25	9.200	2.534	0.787
Spring	30	35	12.33	2.771	0.779
Time since fire (TSF)					
Recent	12	24	11.128	2.638	0.830
Intermediate	24	28	6.774	2.343	0.703
Older	12	29	10.402	2.531	0.752
SOF & TSF					
Spring recent	6	10	2.335	1.379	0.599
Spring intermediate	6	23	8.373	2.438	0.777
Spring older	12	30	4.886	2.134	0.627
Summer recent	12	24	10.148	2.579	0.811
Summer intermediate	12	13	5.474	1.979	0.772

Table 2.7. Average stems of flowering forb species per hectare recorded by years since fire and season of fire over two years in the Joseph H. Williams Tallgrass Prairie Preserve. Vegetation was surveyed in early, mid, and late summer each year.

Plant species	**Spring Recent**	**Spring Intermediate**	**Spring Older**	**Summer Recent**	**Summer Intermediate**
Achillea millefolium	2667	69333	27333	88000	10000
Allium spp.	0	24000	0	0	0
Asclepias tuberosa	0	2667	1333	0	0
Asclepias verticillata	0	0	667	0	0
Asclepias viridiflora	0	667	0	0	0
Asclepias viridis	0	15333	5333	12000	5333
Baptisia bracteata	0	0	1333	0	667
Callirhoe alcaeoides	0	0	0	4000	0
Chamaecrista fasciculata	667	2000	2000	26667	0
Cirsium undulatum	0	1333	0	4000	6667
Convolvulus arvensis	0	0	1333	3333	2667
Coreopsis palmata	2000	0	36667	8000	2667
Dalea purpurea	3333	0	667	0	0
Daucus carota	0	0	40667	77333	0
Dianthus armeria	0	4667	29333	0	0
Dracopis amplexicaulis	0	3333	36667	62667	0
Erigeron spp.	667	23333	50000	37333	35333
Glandularia spp.	0	0	667	0	0
Medicago lupulina	0	0	0	2667	0
Monarda citriodora	0	67333	35333	78000	0
Monarda fistulosa	0	2667	38000	7333	188666
Nemastylis geminiflora	0	0	667	0	0
Oenothera fruticosa	0	3333	2667	2667	0
Oxalis spp.	36667	36667	6000	20000	0
Petalostemum candida	0	667	1333	0	0
Phyla nodiflora	0	2667	0	0	0
Physalis spp.	0	0	0	667	0
Psoralidium tenuiflorum	0	0	667	667	0
Ratibida columnifera	667	10000	1333	24667	10667
Rosa arkansana	0	667	667	0	0
Rubus spp.	1333	36667	51333	0	37333
Ruellia humilis	2667	1333	2667	2667	667
Sabatia campestris	3333	13333	0	0	0
Solanum spp.	0	4000	667	0	0
Solanum rostratum	0	0	0	0	1333
Tradescantia spp.	0	7333	1333	0	0
Trifolium spp.	0	0	2667	12000	0
Vernonia baldwinii	4667	9333	1333	23333	1333
Viola spp.	0	0	1333	0	0

Figures

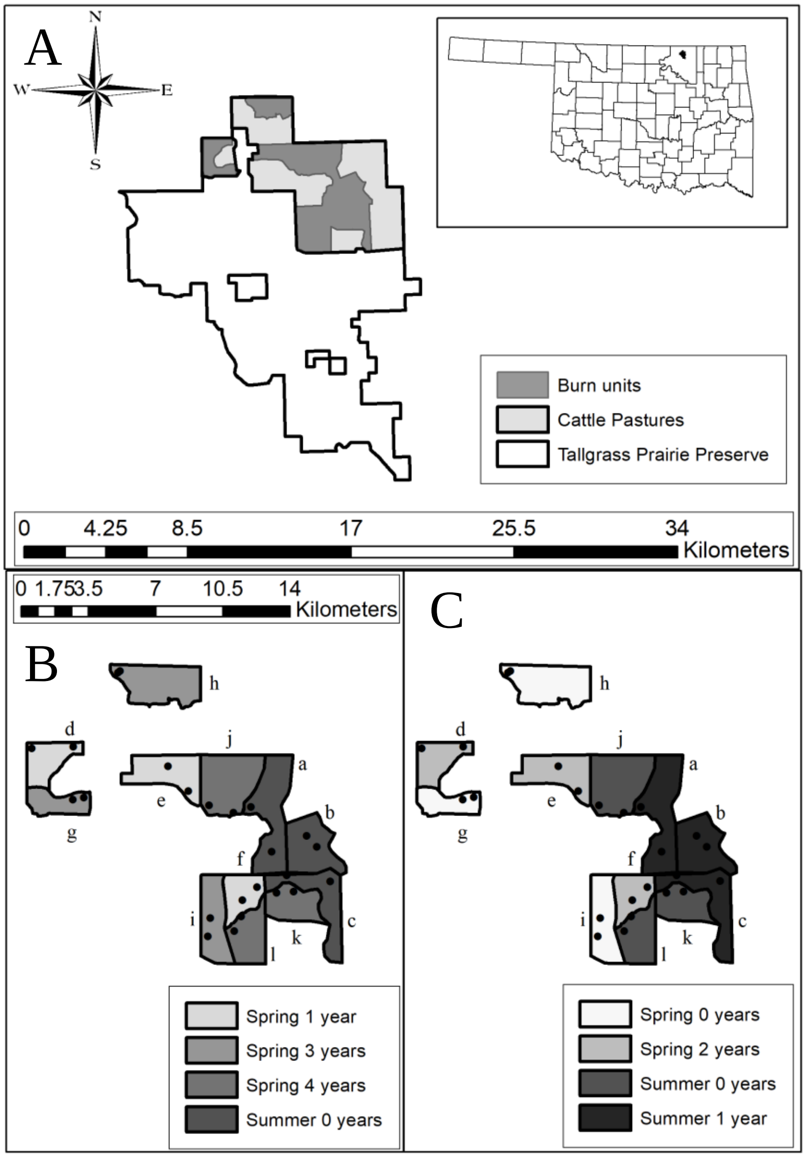

Fig. 2.1. A) Map of burn units in cattle pastures at the Joseph H. Williams Tallgrass Prairie Preserve in northern Oklahoma. **B)** 2019 and **C)** 2020 study sites are outlined by time since fire and season of fire. Burn units are labeled with lower case letters (Table 1). Transect starting points are black circles.

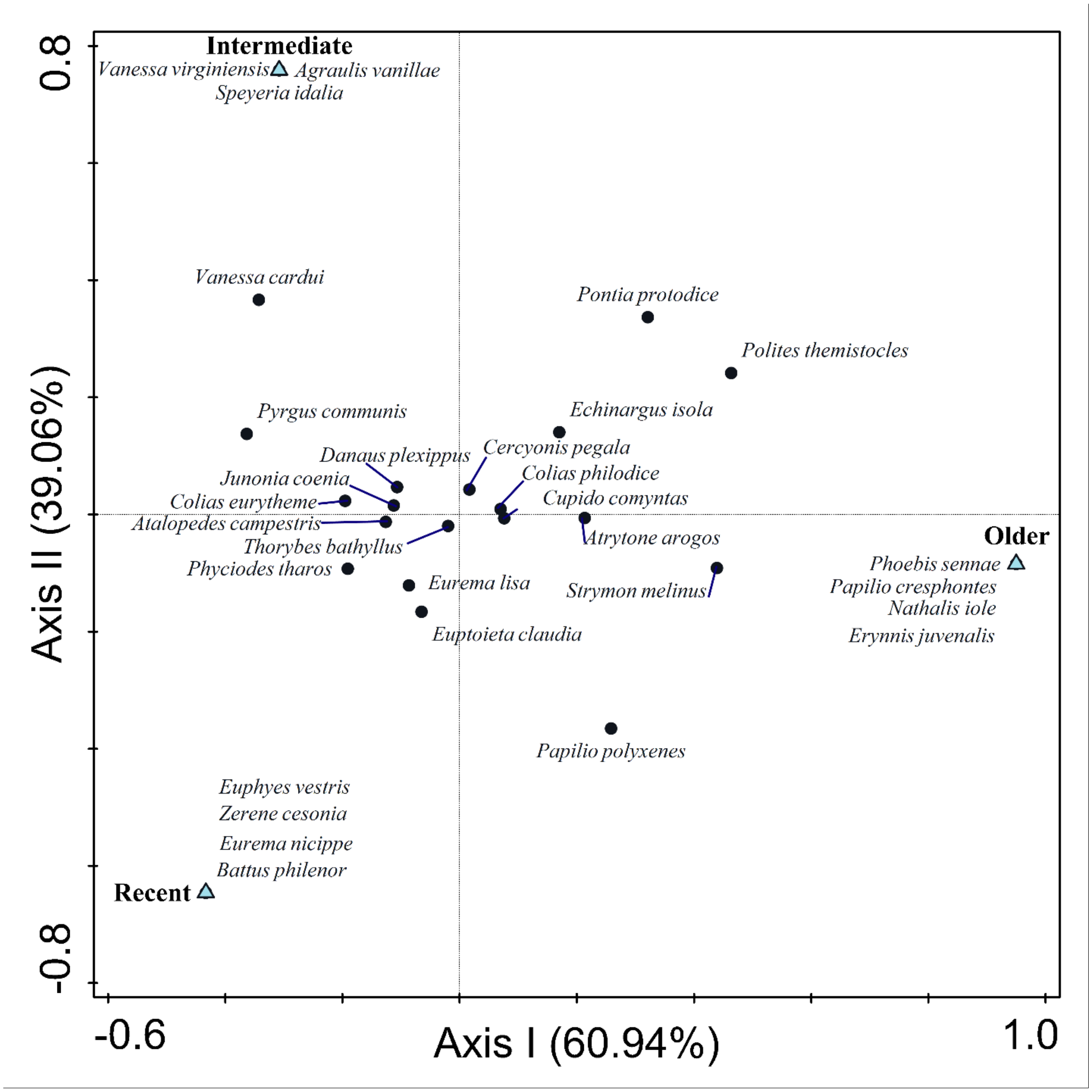

Fig. 2.2. Correspondence analysis ordination diagram of time since fire for the butterfly community. Butterfly species are marked with solid black circles while time since fire is marked with blue triangles. The closer a butterfly species is to a triangle the more abundant it was in sites with that time since fire. Axis I (eigenvalue: 0.198) and Axis II (0.127) explain 100% variance, with the majority from Axis I (60.94%).

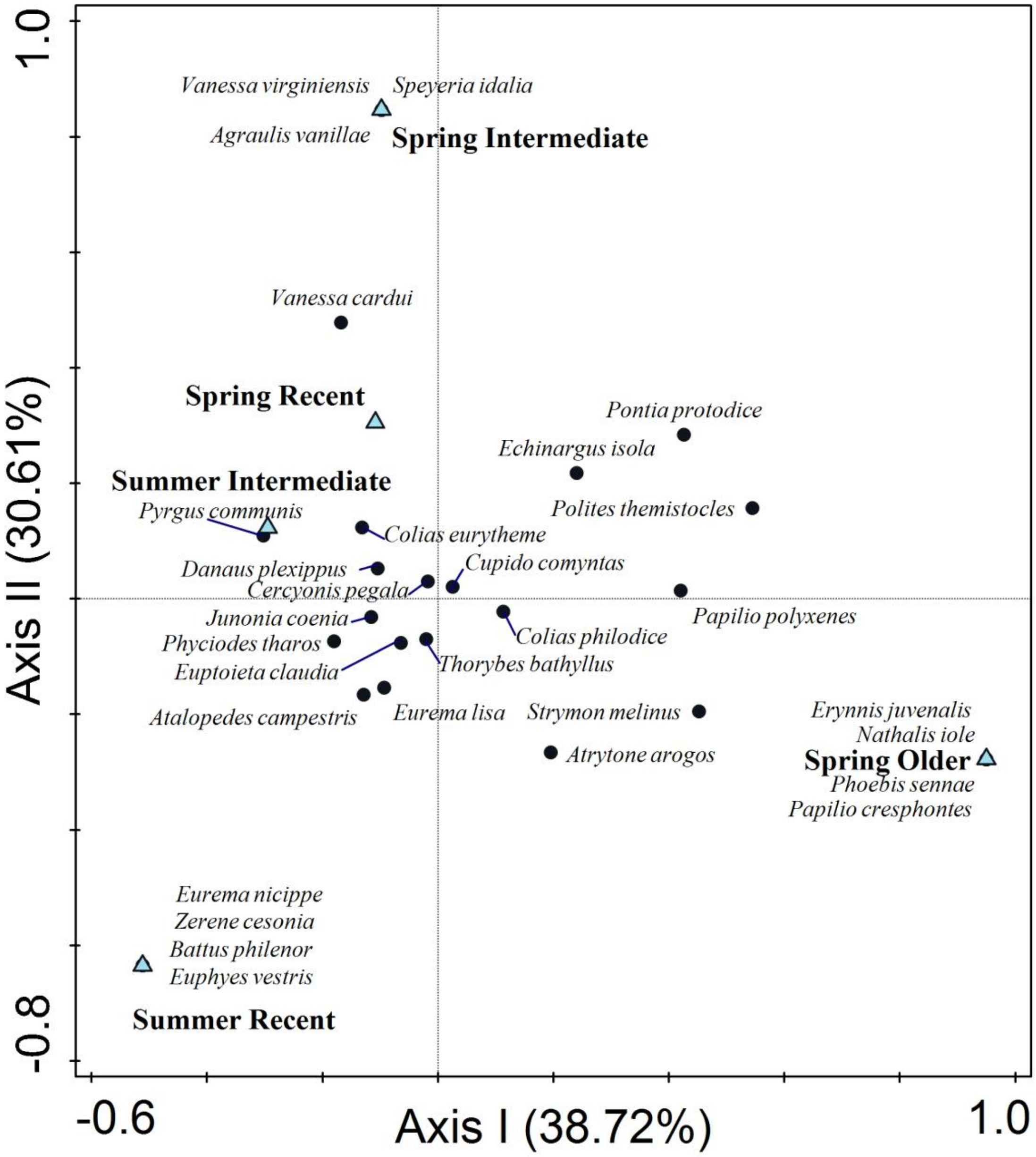

Fig. 2.3. Correspondence analysis ordination diagram of time since fire and season of fire for the butterfly community. Butterfly species are marked with solid black circles while time since fire and season of fire are marked with blue triangles. The closer a butterfly species is to a triangle the more abundant it was in sites with that time since fire and season of fire. Axis I (eigenvalue: 0.204) and Axis II (0.161) explain 69.33% variance, with the majority from Axis I (38.72%).

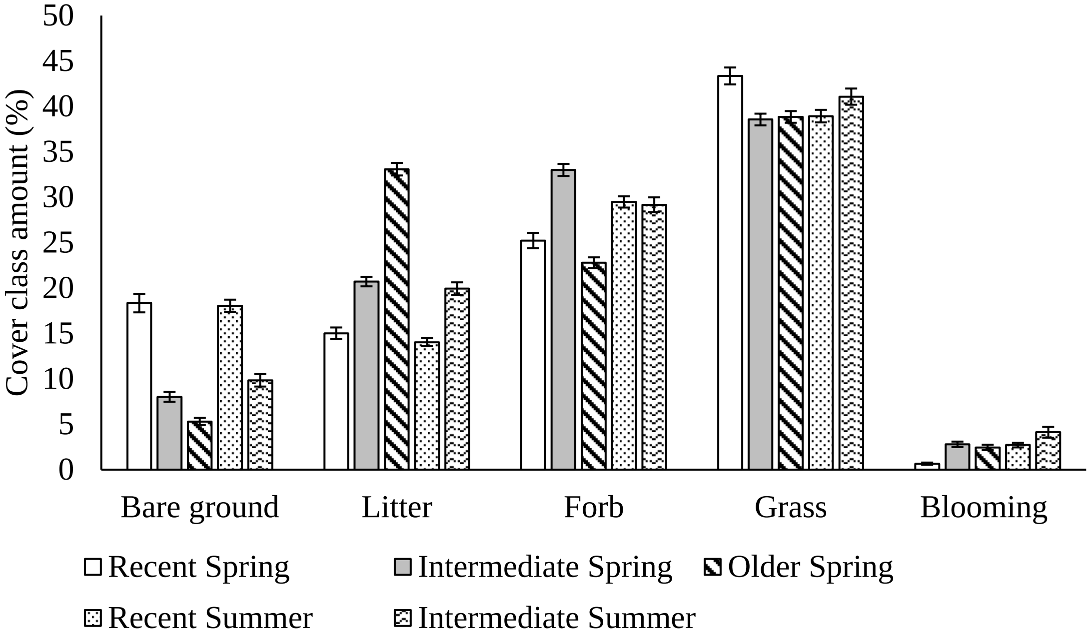

Fig. 2.4. Mean cover classes (bare ground, litter, forb, grass, and blooming forb) by time since fire and season of fire over two years in the Joseph H. Williams Tallgrass Prairie Preserve. Standard error bars are included.

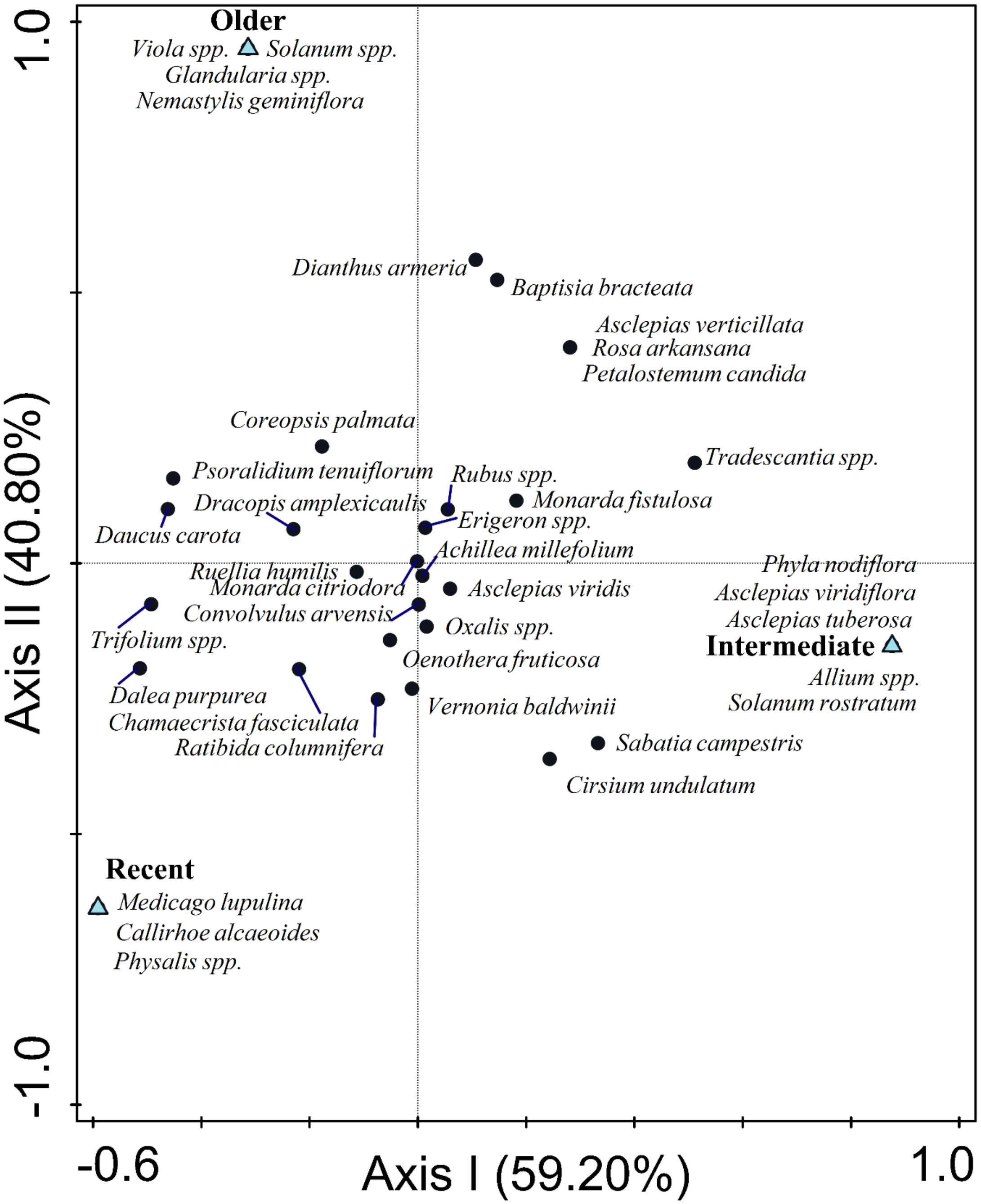

Fig. 2.5. Correspondence analysis ordination diagram of time since fire for the blooming forb community. Plant species are marked with solid circles while time since fire is marked with blue triangles. The closer a species is to a triangle the more abundant it was in sites with that time since fire. Axis I (eigenvalue: 0.199) and Axis II (0.137) explain 100% variance, with the majority from Axis I (59.20%).

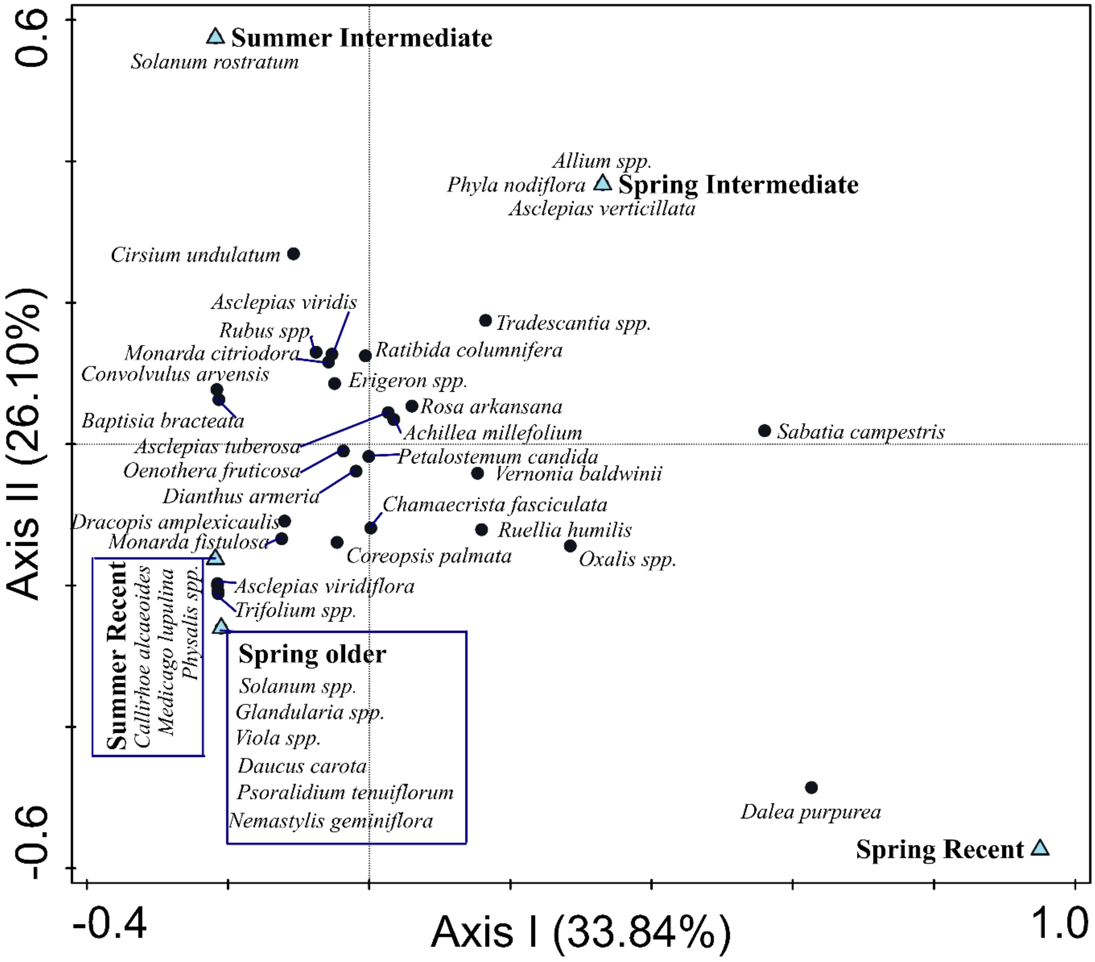

Fig. 2.6. Correspondence analysis ordination diagram of time since and season of fire for the blooming forb community. Plant species are marked with solid circles while time since and season of fire are marked with blue triangles. The closer a species is to a triangle the more abundant it was in sites with that time since and season of fire. Axis I (eigenvalue: 0.245) and Axis II (0.189) explain 59.94% variance, with the majority from Axis I (33.84%).

CHAPTER III

THE EFFECT OF LAND USE INTENSITY AND HABITAT CHARACTERISTICS ON BUTTERFLY COMMUNITY COMPOSITION AND BUTTERFLY COMMUNITY TRAITS WITHIN THE SOUTHERN GREAT PLAINS

Abstract

As grasslands decline grassland dependent species, such as grassland butterflies, undergo widespread population losses. To manage remaining grasslands prescribed fire, grazing, and mowing/haying are commonly implemented management practices across the southern Great Plains. However, the impacts of management and Land Use Intensity (LUI) on butterfly community composition and butterfly community traits are not well studied. Additionally, habitat characteristics such as vegetation height and vegetation cover can alter butterfly communities. To untangle the effects of LUI and habitat characteristics on butterfly community composition and butterfly community traits, we conducted butterfly and flowering forb surveys at grassland sites across north-central Oklahoma. A total of 942 butterflies were recorded across 39 species over two years, with community measures differing by site. Neither LUI nor habitat characteristics had measurable effects on the overall butterfly community composition or butterfly community traits. Similarly, flowering forb community measures differed by site but flowering forb species richness, average flowering stems, and average total flowers per transect did not affect butterfly community composition or butterfly community traits. This research adds to the growing body of literature on butterfly community ecology and highlights the need for further studies to understand what factors drive butterfly community patterns.

Keywords: LUI, landscape, southern Great Plains, prescribed fire, grazing

Introduction

Grasslands have declined by over 90% across North America (Samson and Knopf 1994) leading to grassland dependent species, such as grassland butterflies, undergoing widespread declines. This decline of prairie habitat is due to multiple factors including conversion to row crop agriculture, urban expansion, and habitat degradation due to removal of disturbance regimes, over-grazing, and invasive species encroachment (Samson and Knopf 1994, Swengel and Swengel 1999a, Gornish and Ambrozio dos Santo 2016). To manage remaining grassland fragments, various management strategies are used including grazing, prescribed fire, and mowing/haying (Swengel 2001, Vogel et al. 2007).

Butterfly species vary in their life history traits such as dispersal abilities or overwintering strategies (Scott 1986). In turn, these life history trait differences influence how species respond to management techniques (Swengel 1996). Additionally, butterflies need hostplants for larvae and nectaring plants for adults (Scott 1986) and management strategies can affect these resources in varying ways.

Grazing is part of the evolutionary history of prairies (Anderson 2006, Knapp et al. 1999). Historically, American bison (*Bison bison*) were the dominant grazers in North American prairies but due to the near extirpation of this species, domestic cattle have become the dominant grazers (Anderson 2006, Allred et al. 2011). Cattle graze more intensively and move less than bison and fencing further reduces movement (Freese et al. 2007, Kohl et al. 2013). Grass and forb preferences also vary between cattle and bison which may lead to different butterfly hostplant and nectar plant availability (Everitt et al. 1981, Coppedge et al. 1998). However, research on effects of cattle grazing compared to bison grazing is contradictory with some studies finding effects by cattle grazing on vegetation are similar to those of bison (Towne et al. 2005, Kohl et al. 2013). Butterfly species can respond differently to grazing with some species responding positively due to the presence of shorter vegetation while others respond negatively due to the removal of hostplants (Thomas 1983, Schtickzelle et al. 2007, Vogel et al. 2007). Grazing can alter hostplant structure (Gardner et al. 1997), vegetation canopy cover (Teague et al. 2004, Towne et al. 2005), bare ground availability (Vogel et al. 2007), and oviposition success (Thomas et al. 1986). Additionally, due to differences in livestock stocking rates, seasonality of grazing, and length of time grazers remain in pastures, varying levels of grazing intensity can occur which may affect butterfly responses (Blüthgen et al. 2012, Manley et al. 1997).

Fire is another part of the prehistoric disturbance regime in prairies and helps to maintain the native vegetation community and prevent encroachment by woody species (Rudolph et al. 2006, Guyette et al. 2012). To mimic the natural effects of wildfire, land managers often use prescribed fire. However, fire suppression practices have increased fuel loads and shifted plant species communities from fire-tolerant to fire-intolerant, creating more intense fires (Huntzinger 2003). Prehistorically, wildfires may also have occurred at a lower frequency than prescribed fires in some regions (Swengel 2000). Additionally, prescribed fires can be more detrimental to insect populations if they are restricted to isolated prairie fragments that are burned in their entirety (Swengel 2001, Swengel and Swengel 2007, Black et al. 2011). Some butterfly species such as regal fritillaries (*Speyeria idalia*) are more fire sensitive than others such as gulf fritillaries (*Agrualis vanillae*) (Caven et al. 2017, DeSha 2017). Additionally, the seasonal timing of prescribed fire will influence which part of a butterfly's lifecycle the fire directly affects. The timing of prescribed fires may differ of that for wildfires. Wildfires tend to occur during the hottest driest parts of the year, when prescribed fire is often restricted due to unsuitable weather conditions and burn bans (Roberts et al. 1999, Westerling et al. 2003, Wonkka et al. 2015). Immature stages are more susceptible to mortality from fire due to relative immobility compared to adult butterflies (Swengel 2001, Kral et al. 2017). Furthermore, fire can alter vegetation structure (Bulan and Barrett 1971, Collins and Calabrese 2012), vegetation height (Haysom and Coulson 1998), bare ground availability (Pollak and Kan 1998), hostplant abundance (Adamidis et al. 2019), and nectar plant abundance (Moranz et al. 2014) which may also lead to changes in the butterfly community based on time since fire.

In areas where prescribed fire and grazing do not occur, mowing/haying may be used to prevent grasslands from becoming woody (Feber et al. 1996, Swengel 2001). During haying/mowing, adult butterflies will move to uncut areas while immature life stages may experience higher mortality rates due to relative immobility (Erhardt 1995, Swengel 2001). Total area mowed/hayed can also influence insect populations, with areas that are mowed in portions suffering less detrimental effects than areas that are mowed in their entirety, similar to how burning portions of an area can have less detrimental effects than burning the entirety of an area (Morris and Rispin 1988, Feber et al. 1996, Swengel 2001, Black et al. 2011).

Additionally, sites undergo different frequencies of grazing, burning, and mowing/haying which can make comparative studies challenging. To combat this Blüthgen et al. (2012) developed an additive Land Use Intensity (LUI) index that allows for sites that have undergone variable management regimens to be comparable on a continuous index scale. Sites that undergo higher rates of LUI, i.e. higher rates of disturbance, typically have lower species diversity (Collinge et al. 2003, Börschig et al. 2013). However, grasslands are disturbance-dependent ecosystems and intermittent natural disturbance can help maintain biodiversity (Evans 1984, Erhardt 1985, Anderson 2006, Yuan et al. 2016). Within grasslands, moderate intensity of management can maintain species diversity (Collins and Barber 1986, Kruess and Tscharntke 2002), while increasing intensification of management leads to homogenization of species and the loss of specialist species (Gámez-Virués et al. 2015, Simons et al. 2016).

In addition to management practices and associated LUI, habitat characteristics influence butterfly communities (Öckinger and Smith 2006). Site level traits such as vegetation height, host plant presence, and forb abundance can influence the composition of the butterfly community (Milberg et al. 2016). Broader landscape categorization such as total grassland and surrounding habitat type, can influence the pool of butterfly species available to make up a community at a specific site (Collinge et al. 2003, Villemey et al. 2015). Higher values of LUI can lead to butterfly communities consisting of traits that favor generalist species over traits that favor specialist species (Börschig et al. 2013).

The aims of this study are to investigate how 1) land management in the context of Land Use Intensity, 2) site level habitat characteristics, and 3) broader landscape categorization influence butterfly community composition and butterfly community traits. By untangling the effects of management and habitat characteristics on butterfly communities, context can be provided to ongoing butterfly management recommendations.

Methods

Study Sites

Six grasslands were visited across north-central Oklahoma (Table 1, Fig. S1). This area consists of a mixture of tallgrass prairies and cross-timbers (oak woodlands and open grasslands) with high butterfly species richness including butterfly species of concern such as the regal fritillary (*Speyeria idalia*), Diana fritillary (*Speyeria diana*), dotted skipper (*Hesperia attalus*), Arogos skipper (*Atrytone arogos*), and Byssus skipper (*Problema byssus*; Hamilton 2007; Fisher 2021). These sites included wildlife management areas (WMAs) operated by the Oklahoma Department of Wildlife Conservation and nature preserves that undergo varying management (Table 1). Sites underwent one of four treatments: burning only, burning and haying/mowing, burning and cattle grazing, or burning and bison grazing (Table 1). To compare management among study sites, each study site was defined by the area that encompassed study surveys within a grassland area. At John Dahl WMA, the study site was considered the entirety of the site due to the WMA's smaller size. At The Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve, two smaller areas within the preserve were considered separate study sites due to undergoing different management practices (Table 1). At Kaw WMA, Osage WMA Western Wall Unit, and Osage WMA Rock Creek Unit, study sites were smaller grasslands bordered by woody habitat that occurred within the larger WMAs (Table 1).

Butterfly surveys

For every site, three randomly placed 200 meter transects with random orientation were determined in ArcMap 10.6.1. The initial starting point of each transect was generated using the 'create random point' tool within ArcMap. A buffer was then placed around every point with an additional random point placed within to determine orientation of the transect. Transects were placed ≥ 200 meters apart to prevent sampling the same individuals more than once, located ≥ 50 meters from roads to avoid edge effects, and located within 200 meters from an access point (an area accessible by field vehicle) to minimize logistical constraints (Ries and Debinski 2001, Reeder et al. 2005). The minimum separation distance between transects was 205.74 m, the furthest sites 62.28 km apart, and the study region encompassed a 34,186 hectare area (Table 1, Fig. S1).

Four sites were visited three times during the month of June in 2019 and 2020, for a total of six surveys at each site. Due to flooding in 2019, that prevented a third sampling round Western Wall and Kaw WMA were visited only twice for a total of five surveys over two years. During each site visit, modified Pollard walks were conducted along each transect to record butterfly abundances as far as the eye could see. Pollard walks consisted of walking a standardized fixed route at a slow but consistent pace (Pollard 1977). Pollard walks were modified to count all butterflies that occurred to the sides and ahead of the transect, with care taken to avoid double counting individuals and were identified to species by binoculars (Swengel and Swengel 1999b). Prior to every survey wind speed and temperature were recorded using a handheld Kestrel. Transects were walked between 1000 - 1600 hours Central Daylight Saving Time when temperature was above 13 °C and sunny or if temperatures passed 17 °C regardless of cloud cover

(Pollard 1977, Pollard and Yates 1993, Campbell et al. 2007, Pellet et al. 2012). Transects were not walked if wind speeds surpassed 16 km/h (Moranz et al. 2012). Temperature and wind constraints were chosen because low temperatures and moderate to high winds can inhibit butterfly flight (Pollard 1977, Pollard and Yates 1993).

Butterfly community traits

Life history traits were determined for every butterfly species observed including average wingspan, voltinism (seasonal specialization), hostplant specialization, hostplant category, overall specialization, and overwintering stage (Table S1). Wingspan can reflect dispersal abilities (Sekar 2012), which are important to understanding how migrating species can colonize areas, how species can recolonize areas post-management, and a species' ability to navigate fragmented landscapes (Tscharntke et al. 2002, Lester et al. 2007, Sekar 2012).

Species were designated as seasonal specialists or generalists using Kitahara et al. (2000) definition of multivoltine species (3+ generations per year) as seasonal generalists and oligovoltine species (1-2 generations per year) as seasonal specialists. As species tend to have more generations in the south due to longer warm seasons than in the northern United States, the upper range of generations was used for each species (Scott 1986, Brock and Kaufman 2003). Exposure to management such as prescribed fire during the larval stage may impact a seasonal generalist differently than a seasonal specialist with non-overlapping life stages (Brown et al. 2016). Additionally, seasonal generalist species have more time to recover post-management than seasonal specialist species due to the occurence of more generations (Swengel 1996).

Hostplant specialists typically require areas with consistent and stable hostplant resources while generalists can also occupy areas with more unreliable resources because they can utilize more hostplant species (Wiklund 1981, Wiklund 1982, Futuyma and Moreno 1988, Kitahara et al. 2000, Kassen 2002). Known families and genera of hostplants were counted for every species observed (Scott 1986). The definition of host plant specialist was broadend for this study because few butterfly species in North America are true monophagous specialists (using only one species of hostplant). Species that used 10 or fewer genera within one plant family were considered hostplant specialists (narrow oligophagous) while those that used more than 10 genera within one plant family (broad oligophagous) or used genera in multiple plant families (polyphagous) were both considered hostplant generalists (Wiklund 1982, Kitahara et. al 2000). Because management can influence the vegetation structure of hostplants, butterfly species were also divided into broad categories based on hostplants including grasses, forbs, sedges, trees, and shrubs (Collin 1987, Towne et al. 2005, Collins and Calabrese 2012). Butterflies were additionally categorized as either a true specialist (both seasonal and hostplant specialist), true generalist (both seasonal and hostplant generalist) or as an intermediate (either hostplant specialist/seasonal generalist or hostplant generalist/seasonal specialist) (Kitahara et. al 2000).

Finally, overwintering strategies were included for every species because they can influence the presence of a species (Swengel 2001, Kral et al. 2017). Overwintering in the egg stage is dependent on species-specific strategies such as the female laying eggs on woody hostplants or near known forb hostplant patches or dropping eggs at random (Wiklund 1984). To overwinter as larvae, species often burrow into soil, leaf litter, or grass clumps and then remain stationary until spring (Gilbert and Singer 1975, Schultz and Crone 1998). For species that overwinter as pupae, larvae often choose locations for pupation that provide protection from winter elements and predation (Brakefield et al. 1992, Stefanescu 2004). For overwintering adults, species tend to have various supercooling abilities that can allow an individual to survive temporary freezes (Pullin and Bale 1989). Migratory species depend on adults recolonizing areas from warmer regions every spring. Species that overwinter in immature stages, in comparison, depend on the adults of the prior generation colonizing that area. This difference in overwintering strategies may influence the presence of different species.

Land Use Intensity index

A Land Use Intensity index value was calculated for every study site for each year. Blüthgen et al. (2012) proposed an additive compound index to measure Land Use Intensity over three variables (fertilization frequency, grazing intensity, and mowing/haying frequency) presented as:

$$L_i = \frac{F_i}{F_r} + \frac{M_i}{M_r} + \frac{G_i}{G_r}$$

Where F = fertilization, M = mowing/haying, G = livestock grazing, and L = Land Use Intensity. To modify the equation to be relevant to the study region where grasslands are typically not fertilized and prescribed fire is a common management strategy, F_i was replaced with B_i, the frequency of burning per year:

$$L_i = \frac{B_i}{B_r} + \frac{M_i}{M_r} + \frac{G_i}{G_r}$$

Mowing/haying frequency was calculated the same as in the original equation with M_i the frequency of mowing/haying per year. To calculate grazing intensity Animal Units (AU) per acreage (Gi= AU/acre) were used. Animal Units are a standard unit of livestock stocking rate used in rangeland management in North America, especially within the southern Great Plains where the majority of land has a history of being privately owned and stocked with cattle (Reeves and Baggett 2014). Animal Units reflect the potential intensity of grazing by livestock by incorporating livestock weight in the measurement (Scarnecchia 1985, Hinnant 1994). As in the original equation, all variables were standardized by the respective means of that region (B_r, M_r, G_r). As suggested in Blüthgen et al. (2012) the LUI was calculated as the average of each study year as well as the previous two years to get a more accurate representation of the LUI that is occurring within each study site.

Habitat characteristics

Vegetation data were recorded after each Pollard walk to avoid disturbing butterflies before the walk. Vegetation height was measured every 20 meters along the 200m transect by recording the highest point the vegetation touched on a ruler. For every 10 meters of each transect, we placed a 0.5m x 2m quadrat was placed over vegetation. Cover data were estimated for every quadrat using a modified Daubenmire cover class system (1 = <5%, 2 = 5-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, 6 = >95%) to determine bare ground, litter, forb, grass, and woody cover (Daubenmire 1959). Additionally, percentage of blooming forbs and non-blooming forbs were recorded per quadrat. Within every quadrat, total flowering forb counts and species were recorded to capture nectar availability.

Broader landscape categorization

All sites were digitized in ESRI ArcMap 10.6.1 to estimate total area. To investigate broad landscape differences, all sites were classified into land use categories. The Oklahoma Department of Wildlife Conservation provided detailed GIS vegetation raster data (pers. comm. Keith Waag). For ease of analysis, vegetation categories within the vegetation raster data were combined into eleven broader categories, such as barren, riparian barren, and bottomland barren all being grouped under a broad barren category (Table S2).

Three buffers (0.5 km, 1 km, and 1.5 km) were placed around each transect within ArcMap to determine broad habitat characteristic differences (Davis et al. 2007). Buffer widths were chosen to capture landscape differences that may influence butterflies at different spatial scales (Davis et al. 2007). Within every buffer, percentage of land use categories were calculated per site (Table S3).

Analysis

To compare sites, community measures (species richness, Shannon-Wiener diversity index, Inverse Simpson diversity index, and Pielou's evenness) were calculated for both butterflies and flowering forbs (R Core Team 2020, version 3.3.2, R package Vegan, Morris et al. 2014). Diversity indices emphasize frequencies of species differently, so both a Shannon-Wiener Index and inverse Simpson's Index of Diversity were calculated for each treatment (Morris et al. 2014). Inverse Simpson's Index of Diversity (1/D) adds more weight to abundant species while the Shannon-Wiener Index (H') adds equal weight to rare and abundant species (Morris et al. 2014). In comparison, species richness (S) applies the same level of influence to a species regardless of total individuals counted, therefore emphasizing rare species (Morris et al. 2014). To measure the relative abundance of species in an area, Pielou's evenness (J') was calculated (Collinge et al. 2003, Vandermeer 1981). The use of all four measures allows for a more accurate representation of the diversity, evenness, and richness within a community.

A non-metric multidimensional scaling (NMDS) ordination diagram was used to compare the butterfly community along two dimensions using species abundance and to compare similarities between years and management types. We used the Bray-Curtis coefficient within package vegan in R to calculate dissimilarity indices (R Core Team 2020).

To determine how butterfly community composition was impacted by LUI index values, habitat characteristics, and broader landscape categorization, multivariate generalized linear models (GLMs) with negative binomial distributions were run using R packages mvabund and lattice (Sarkar 2008, Wang et al. 2012, R Core Team 2020). Within package mvabund, the function ANOVA produces an analysis-of-deviance table with likelihood ratio test values and resampled p-values. For this analysis, p-values underwent 1000 resampling iterations (Wang et al. 2012).

To investigate the relationships between butterfly community traits and LUI index values, habitat characteristics, and broader landscape categorization, a fourth-corner analysis was conducted in R package ade4 (Börschig et al. 2013, R Core Team 2020). A fourth-corner analysis allows relationships between species traits and environmental traits to be compared by using the community data that is shared between the datasets as a commonality link (Börschig et al. 2013). For traits that were categorical, a numeric value was assigned to each category for ease of analysis (Stevens et al. 2012, Börschig et al. 2013; Table S1).

Results

Across two years, a total of 942 butterflies were recorded from 39 species, with 6 undientified butterflies in 2019 (Table S4). The most commonly observed species were eastern tailed blues (*Cupido comyntas*) (n = 259) and orange sulphurs (*Colias eurytheme*) (n = 117) that made up 39.92% of all butterflies seen (Tables 2, S4). Out of the total 39 species, 24 species were seen both years and seven were seen at all six sites (Table 2). Six of these species (*Colias eurytheme*, *Cupido comyntas*, *Euptoieta claudia*, *Junonia coenia*, *Pontia protodice*, and *Strymon melinus*) were categorized as true generalists while *Eurema lisa* is categorized as intermediate (Table S5). Seven species were only seen once (i.e., during one survey at one site; Table 2) over the two years with four categorized as intermediate (*Epargyreus clarus*, *Erynnis funeralis*, *Satyrium calanus*, and *Zerene cesonia*), two as true specialists (*Anaea andria* and *Protographium marcellus*), and one as a generalist (*Battus philenor*) (Table S5). One true specialist (*Cercyonis pegala*) was recorded at five of the six sites, while the remaining eight specialist species were seen at either one or two sites each (Tables 2, S5).

Community measures differed by site with both units at the Tallgrass Prairie Preserve having the highest species richness (2019: Bison Unit S= 19; 2020: Nature Trail Area S=23) while units at Osage WMA had the lowest species richness both years (2019:

Western Wall S=11; 2020: Rock Creek S=14; Table 3). The Nature Trail Area had the most butterflies recorded with a total of 264 butterflies over two years while Western Wall had the fewest with 62 butterflies (Table 3). The Nature Trail Area had the most specialist species (*Cercyonis pegala*, *Erynnis juvenalis*, *Lycaena dione*, *Speyeria cybele*, and *S. diana*) while Rock Creek had the fewest specialist species (*Anaea andria*) (Tables 2, S5). Diversity indices also varied by site by year. Both Tallgrass Prairie Preserve units had the highest Shannon-Wiener diversity index of the six sites (both H = 2.357) in 2019, and in 2020 the Nature Trail Area continued to have the highest Shannon-Wiener diversity index (H = 2.565; Table 3). Rock Creek had the lowest Shannon-Wiener diversity index in 2019 (H = 1.914) and John Dahl WMA had the lowest in 2020 (H =1.906; Table 3). Western Wall had the highest inverse Simpson diversity index both years (2019: 1/D = 0.891; 2020: 1/D = 0.901; Table 3). Rock Creek had the lowest inverse Simpson diversity index in 2019 (1/D = 0.739) and John Dahl WMA had the lowest in 2020 (1/D =0.754) (Table 3). Western Wall had the highest Pielou's evenness values for both years (2019: J' = 0.979; 2020: J' = 0.878; Table 3). John Dahl WMA had the lowest Pielou's evenness values in 2019 (J' = 0.736) while Rock Creek had the lowest in 2020 (J' = 0.707; Table 3).

The NMDS ordination diagram had a stress value of 0.16, which suggests a good representation of the data within the 2-dimensionsial space (Clarke 1993,Tyler and Kowalewski 2014). The diagram showed differences in the butterfly communities by management type and year. Year was separated into two distinct groups with species recorded in 2020 along the more positive portion of axis II and species recorded in 2019 along the more negative portion of axis II. Sites that had undergone burning and cattle grazing also separated out into a distinct cluster along the more positive portion of axis I, while the other three management types (burning, burning/haying, and burning/bison grazing) overlapped along the more negative portion of axis I.

Land Use Intensity index values had no effect on overall butterfly community composition (2019: LRT = 52.78, $p = 0.158$; 2020: LRT = 58.12, $p = 0.236$) or butterfly community traits (all $p > 0.05$; Table 4). Similarly, habitat characteristics including vegetation cover categories, blooming forb percentage, vegetation height, and soil moisture had no impact on butterfly community composition or community traits (all $p > 0.05$, Tables 5, 6). Finally, broad landscape categorization at all three spatial scales had no signifcant effect on either the butterfly community composition or community traits (all $p > 0.05$, Tables 7, 8, S6-7).

Flowering forbs differed by site by year with the Tallgrass Prairie Preserve Bison Unit having the highest species richness in 2019 (S=19) and Rock Creek and the Tallgrass Prairie Preserve Bison Unit having the highest species richness in 2020 (both S=11; Table S8). In 2019, Kaw WMA had the highest average flowering stems (4.701 ± 0.56) while the Nature Trail Area had the highest average total flowers per transect (13.474 ± 7.55; Table S8). Overall, there were fewer blooming forbs in 2020. The Bison Unit had the most flowering stems per transect (1.157 ± 0.26) and Kaw WMA had the most flowers per transect (12.508 ± 2.24; Table S8) in 2020. The site with the fewest flowering stems in 2019 was Western Wall (1.773 ± 0.30) with the John Dahl WMA having the fewest flowers per transect (3.571 ± 1.66; Table S8). In 2020 John Dahl WMA had both the fewest flowering stems (0.033 ± 0.03) and flowers per transect (0.033 ± 0.03; Table S8). Despite these differences, flowering forb species richness, average flowering stems, and average total flowers per transect did not affect butterfly community composition nor butterfly community traits (Tables 5, S9).

Discussion

Community measures differed by site for butterflies and forbs, but these differences were not explained by LUI, habitat characteristics, or landscape categorization. The Tallgrass Prairie Preserve units consistently had the highest butterfly species richness, Shannon-Wiener diversity indices, and abundances while the Osage WMA units consistently had the lowest species richness and abundance. One key difference between these sites were the LUI values. Even small differences in LUI can alter invertebrate diversity (Weiner et al. 2011). Both Tallgrass Prairie Preserve units had lower LUI values than the Osage WMA units. However, there were sites with both higher and lower LUI values than either Tallgrass Prairie Preserve units or Osage WMA sites. While these LUI extremes did not appear to be reflected in butterfly community measures, they did match flowering forb presence with the site with the lowest LUI (John Dahl WMA) having the lowest average number of flowering stems both years, while the site that had the highest LUI value (Kaw WMA) had the highest average number of flowering stems in 2019, and the highest flowers per transect in 2020. Land Use Intensity is an additive compound formula that allows for comparison among sites that undergo variable management frequencies and techniques (Blüthgen et al. 2012).

Looking at individual components of management, John Dahl WMA had the lowest rate of prescribed fire while Kaw WMA had the highest frequency of prescribed fire. Despite having low Shannon-Wiener diversity indices score in 2019, Rock Creek had the highest inverse Simpson diversity index. Inverse Simpson diversity adds more weight to abundant species while Shannon-Wiener diversity index adds equal weight to abundant and rare species, which may account for the differences between the two diversity indices (Nagendra 2002, Morris et al. 2014). Butterfly communities in areas that had undergone prescribed burning with cattle grazing were dissimilar from other management types. For sites that had undergone burning and mowing, this is not unusual as Ditlhogo et al. (1992) found little difference in invertebrate communities between fire-managed sites and sites managed by mowing/haying. There are few studies on the impacts of livestock grazing and prescribed fire on arthopods, but Moran (2014) found arthropod abundance and diversity increased on prairies managed with bison and burning. For cattle- and burn-managed sites, Moranz et al. (2012) found that prairie specialist butterflies responded more negatively to burned pastures with cattle grazing compared to pastures that were only burned. These differences in presence of specialist and generalist species may have led to the separation of cattle grazing and burning managed from the other three management methods.

In this study LUI had no effect on butterfly community composition or on traits. This contrdicts Börschig et al. (2013) who found that generalist traits became more common with increasing LUI. Similar to Börschig et al. (2013), neither feeding niche nor wing length were impacted by LUI. Generations per year and overwintering stage were not influenced by LUI, whereas Börschig et al. (2013) found that as LUI increased, generalist traits of mutlivoltinism and overwintering as adults/migrating also increased in butterfly communities. Similarly, Perović et al. (2015) found that migratory tendency increased with increasing LUI values. One potential reason for these differences was that management at our sites had more variation and had higher levels of LUI (range of 0.27-

8.23 LUI in 2019 and 0.36-8.42 LUI in 2020) compared to Börschig et al. (2013), which ranged from 0.5-3.5 LUI. As the majority of our sites had LUI index values >2.0, high rates of disturbance across the sites may have already removed disturbance-sensitive species and specialist favored traits from the butterfly community prior to the start of the study (Blair and Launer 1997, Kitahara et al. 2000). All of our sites have been undergoing the same management regimen for at least 7 years with some sites using the current management regimen for more than 15 years. Additionally, overall low sampling numbers may have prevented differences within communities being detected as was similarly seen by Börschig et al. (2013).

Habitat characteristics had no influence on butterfly community composition and traits. In contrast, Davis et al. (2007) found that litter can influence the butterfly community with disturbance-tolerant butterflies responding negatively to litter and habitat-sensitive species responding positively. However, Davis et al. (2007) recorded butterfly abundances of 0.10 butterflies per meter walked (1057 butterflies, 11,100 meters) compared to our study that recorded 0.05 butterflies per meter walked (942 butterflies, 20,400 meters). Vogel et al. (2007) also found that butterflies can respond negatively or positively to bare ground and vegetation cover depending on the species. However, Vogel et al. (2007) also recorded more individual butterflies over two years (4,000 butterflies, 17,250 m^2) compared to our study that recorded 942. Similarly, both Moranz et al. (2012) and Bendel et al. (2018) recorded over 2,500 individuals over two years during the growing season in upper Midwest grasslands with a rate of 0.36 butterflies per meter walked (2,842 butterflies, 7,800 meters) and 0.27 butterflies per meter walked (2,578 butterflies, 9,600 meters) respectively. Our lower numbers may reflect regional differences in butterfly community responses at our study location. Finally, broad landscape categorization had no influence on butterfly community composition or butterfly traits. As all sites were similar at all three spatial scales (0.5 km, 1 km, and 1.5 km) this may have led to similar results among spatial scales. This is similar to what Davis et al. (2007) found with butterfly communities correlated at 0.5-km, 1.0-km, 1.5-km, and 2.0-km extents but with no extent more correlated than another. However, the highest average percentage of grassland in Davis et al. (2007) was 26.86% at 0.5-km. In comparison, our sites were dominated by grasslands with average grassland at sites ranging from 50-98% based on extents (Table S3).

In conclusion, our research contributes to the growing body of literature on the effects of landscape management on native butterfly species community composition and traits. For species in the southern Great Plains, further research is needed to untangle the effects of LUI and habitat characteristics on butterfly communities. Additionally, the use of a modified LUI, as in Blüthgen et al. (2012), recommended for the southern Great Plains due to the ability to measure different types and frequencies of management on a consistent scale. The LUI equation weights grazing equally with other variables however, grazing intensity is not only dependent on total animals within a pasture but the length of time animals are allowed to graze within a pasture. Adding a time component to the grazing variable to control for grazing time in addition to total animals could help increase the accuracy of the grazing variable. Similarly, timing of management is not accounted for in the equation and adding a seasonal component could further improve the Blüthgen et al. (2012) LUI equation. However, further research is needed on the effects of management timing and grazing timing on the butterfly community to accurately adjust the equation. Combining LUI with a working knowledge of species natural histories can create a comparative way to evaluate grassland butterflies across varied landscapes (Blüthgen et al. 2012, Börschig et al. 2013).

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Tables

Table 3.1. Study sites, total area of site, area of management unit, land manager, and management strategies. Management unit sites: BU= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Bison Unit, NT= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Nature Trail Area, RCU= Osage WMA Rock Creek Unit, and WWU= Osage WMA Western Wall Unit. Land manager: TNC= The Nature Conservancy and ODWC= Oklahoma Department of Wildlife Conservation.

Site name	**Site size (ha)**	**Management unit size (ha)**	**Survey area size (ha)**	**Management strategies**	**Land Manager**
John Dahl WMA	194	194	194	Burning	ODWC
Joseph H. Williams Tallgrass Prairie Preserve	15,700	BU: 9886 NT: 352	1619 352	Burning and bison grazing Burning	TNC
Kaw WMA	6578	6578	64	Burning and mowing/haying	ODWC
Osage WMA	3914	RCU: 1506 WWU: 2408	442 365	Burning and cattle grazing Burning and cattle grazing	ODWC

Table 3.2. List of total butterflies by species seen by study site from 2019 and 2020 summers. Sites: BU= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Bison Unit, JD =John Dahl Wildlife Management Area (WMA), KAW= Kaw WMA, NT= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Nature Trail Area, RCU= Osage WMA Rock Creek Unit, and WWU= Osage WMA Western Wall Unit.

Family & Species	**BU**	**JD**	**KAW**	**NT**	**RCU**	**WWU**	**Total sites**
Hesperiidae							
Achalarus lyciades	0	0	0	0	2	0	1
Anatrytone logan	0	1	1	0	0	0	2
Atalopedes campestris	1	0	1	0	0	0	2
Atrytone arogos	4	0	16	1	1	3	5
Epargyreus clarus	0	0	0	0	0	1	1
Erynnis funeralis	0	0	0	0	1	0	1
Erynnis juvenalis	1	0	0	2	0	0	2
Euphyes vestris	1	0	2	0	0	1	3
Polites themistocles	0	1	5	1	6	5	5
Pyrgus communis	1	1	5	1	0	1	5
Thorybes bathyllus	0	2	0	4	3	0	3
Wallengrenia otho	0	0	2	0	0	0	1
Lycaenidae							
Cupido comyntas	33	74	52	38	50	12	6
Echinargus isola	1	14	0	1	4	0	4
Lycaena dione	0	1	0	2	0	0	2
Satyrium calanus	0	0	0	1	0	0	1
Strymon melinus	1	7	11	13	4	1	6
Nymphalidae							
Anaea andria	0	0	0	0	1	0	1
Cercyonis pegala	4	2	2	27	0	1	5
Danaus plexippus	13	17	11	36	7	5	6
Euptoieta claudia	5	2	19	17	8	2	6
Junonia coenia	6	10	9	27	9	5	6
Phyciodes tharos	1	0	6	14	8	4	5
Speyeria cybele	0	0	0	3	0	0	1
Speyeria diana	0	0	0	1	0	1	2
Vanessa cardui	2	2	0	5	0	0	3
Vanessa virginiensis	2	2	2	6	0	1	5
Papilionidae							
Battus philenor	1	0	0	0	0	0	1
Papilio cresphontes	3	0	0	0	0	3	2
Papilio polyxenes	10	0	1	4	7	8	5
Protographium marcellus	1	0	0	0	0	0	1
Pieridae							
Colias eurytheme	31	14	35	29	5	3	6

Colias philodice	1	2	1	2	0	0	4
Eurema lisa	5	3	2	22	1	3	6
Eurema nicippe	2	0	2	1	0	0	3
Nathalis iole	1	3	1	0	0	0	3
Phoebis sennae	0	0	0	1	1	1	3
Pontia protodice	8	7	1	5	1	0	5
Zerene cesonia	0	0	0	0	0	1	1
Unknown	1	0	0	2	0	3	
Total species	25	19	22	26	17	21	
Total individuals	139	165	187	264	119	62	

Table 3.3. Butterfly community measures (species richness, Shannon-Wiener diversity, inverse Simpson diversity, and Pielou's evenness) for six study sites in north-central Oklahoma. The land use intensity (LUI) index values are included for each site. Sites: BU= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Bison Unit, JD= John Dahl Wildlife Management Area (WMA), KAW= Kaw WMA, NT= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Nature Trail Area, RCU= Osage WMA Rock Creek Unit, and WWU= Osage WMA Western Wall Unit. Highest values bolded.

Site	**Species Richness (S)**		**Shannon-Wiener Diversity (H)**		**Inverse Simpson Diversity (1/D)**		**Pielou's Evenness (J')**		**Species abundance (N)**		**Land Use Intensity Index Values**	
	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020
BU	**19**	16	**2.357**	2.362	0.841	0.854	0.799	0.845	79	60	1.995	1.950
JD	14	15	1.993	1.906	0.767	0.754	0.736	0.719	74	91	0.364	0.267
KAW	13	17	2.048	2.340	0.808	0.868	0.776	0.708	101	86	**8.419**	**8.225**
NT	16	**23**	**2.357**	**2.565**	0.876	0.897	0.853	0.760	**112**	**152**	1.156	0.962
RCU	12	14	1.914	2.284	0.739	0.855	0.746	0.707	56	63	2.708	2.951
WWU	11	15	2.342	2.512	**0.891**	**0.901**	**0.979**	**0.878**	29	33	3.359	3.646

Table 3.4. The effect of land use intensity (LUI) on six butterfly community traits in north-central Oklahoma using a fourth-corner analysis. Values are presented as *r* (correlation coefficient), *p*.

Trait	**LUI 2019**		**LUI 2020**	
	r	*P*	*r*	*P*
Average wingspan	-0.085	0.419	0.042	0.703
Voltinism	0.069	0.499	0.048	0.587
Hostplant specialization	-0.031	0.780	-0.038	0.747
Hostplant category	0.030	0.828	0.050	0.611
Overall specialization	-0.014	0.924	0.006	0.946
Over-wintering stage	0.063	0.579	0.035	0.790

Table 3.5. The effect of habitat characteristics and flowering forbs on butterfly community composition in north-central Oklahoma using multivariate generalized linear models using negative binomial distribution. Likelihood ratio test values (LRT) and p-values (*p*) are reported for each variable by year.

Variable	**LRT**	***p***
2019		
Bare ground cover %	33.13	0.51
Litter cover %	48.88	0.17
Forb cover %	37.21	0.35
Grass cover %	42.91	0.34
Woody cover %	52.98	0.24
Blooming cover %	36.58	0.40
Vegetation height (cm)	36.82	0.40
Soil moisture	48.40	0.24
Flowering species richness (N)	34.00	0.47
Average flowering stems	36.43	0.42
Average total flowers	35.48	0.43
2020		
Bare ground cover %	46.51	0.37
Litter cover %	71.87	0.16
Forb cover %	60.26	0.22
Grass cover %	55.74	0.26
Woody cover %	47.56	0.33
Blooming cover %	53.30	0.36
Vegetation height	41.86	0.50
Soil moisture	45.63	0.41
Flowering species richness (N)	31.36	0.61
Average flowering stems	53.44	0.28
Average total flowers	51.61	0.32

Table 3.6. The effect of site level habitat characteristics on six butterfly community traits in north-central Oklahoma using multivariate generalized linear models with negative binomial distributions. Values are reported as Likelihood ratio test values (LRT) and p-values for each variable (LRT, *p*). BG= bareground, LT= litter, F= forb, G= grasses, W= woody, BM= blooming forb cover, VH= vegetation height, and SM= soil moisture.

2019

Trait	**BG %**	**LT %**	**F %**	**G %**	**W %**	**BM %**	**VH**	**SM**
Average wingspan	0.008, 0.866	-0.122, 0.384	-0.055, 0.713	0.0456, 0.634	0.099, 0.604	-0.075, 0.353	0.047, 0.708	0.072, 0.659
Voltinism	-0.054, 0.367	0.043, 0.603	-0.035, 0.511	0.019, 0.830	-0.001, 0.980	0.053, 0.465	0.035, 0.781	-0.010, 0.930
Hostplant specialization	0.074, 0.548	0.092, 0.545	0.102, 0.502	-0.044, 0.733	-0.143, 0.458	-0.070, 0.528	-0.147, 0.190	-0.129, 0.415
Hostplant category	0.056, 0.863	0.167, 0.266	0.191, 0.227	-0.079, 0.721	-0.024, 0.157	0.023, 0.910	-0.183, 0.172	-0.177, 0.248
Overall specialization	0.057, 0.616	0.095, 0.500	0.088, 0.560	-0.037, 0.771	-0.134, 0.472	-0.054, 0.606	-0.130, 0.222	-0.123, 0.427
Over-wintering stage	0.020, 0.938	0.139, 0.300	0.118, 0.430	-0.016, 0.943	-0.200, 0.285	0.008, 0.931	-0.112, 0.436	-0.192, 0.205

2020

Trait	**BG %**	**LT %**	**F %**	**G %**	**W %**	**BM %**	**VH**	**SM**
Average wingspan	-0.144, 0.369	-0.063, 0.647	0.017, 0.884	0.103, 0.507	-0.029, 0.842	0.106, 0.361	0.049, 0.714	-0.027, 0.825
Voltinism	-0.101, 0.498	-0.081, 0.459	0.020, 0.879	0.095, 0.486	0.123, 0.165	0.031, 0.761	0.109, 0.310	-0.087, 0.317
Hostplant specialization	0.188, 0.240	0.087, 0.489	-0.053, 0.676	-0.119, 0.458	-0.060, 0.577	-0.094, 0.467	-0.097, 0.447	0.048, 0.668
Hostplant category	-0.097, 0.514	-0.122, 0.270	-0.013, 0.842	0.145, 0.273	0.036, 0.785	0.055, 0.613	0.115, 0.304	-0.075, 0.419
Overall specialization	0.058, 0.777	0.019, 0.886	-0.029, 0.643	-0.022, 0.925	0.019, 0.860	-0.029, 0.868	0.000, 0.994	-0.022, 0.758
Over-wintering stage	-0.174, 0.281	-0.130, 0.280	0.041, 0.776	0.153, 0.295	0.149, 0.130	0.052, 0.700	0.178, 0.102	-0.098, 0.362
Average wingspan	0.085, 0.665	0.063, 0.635	0.042, 0.752	-0.114, 0.459	0.095, 0.402	-0.132, 0.261	0.011, 0.947	0.056, 0.610

Table 3.7. The effect of land use categories on butterfly community composition at spatial scales of 0.5 km, 1.0 km, and 1.5 km in north-central Oklahoma using multivariate generalized linear models using negative binomial distribution. Likelihood ratio test values (LRT) and p-values (*p*) are reported for each variable by year. There was no disturbed habitat at spatial scale 0.5km.

Variable	**0.5 km**		**1.0 km**		**1.5 km**	
	LRT	***p***	**LRT**	***p***	**LRT**	***p***
2019						
Agriculture	36.11	0.33	46.56	0.21	46.56	0.21
Barren	49.45	0.16	27.37	0.55	2726	0.55
Disturbed	--------	---------	49.45	0.15	59.05	0.12
Forest	41.18	0.35	36.11	0.43	40.27	0.33
Grasslands	52.86	0.19	33.87	0.47	33.40	0.48
Shrublands	46.42	0.22	54.85	0.21	64.94	0.10
Unassigned	44.64	0.35	48.06	0.31	38.72	0.43
Urban	45.72	0.25	36.73	0.37	26.70	0.60
Water	57.88	0.15	28.58	0.57	49.85	0.15
Wetland	39.71	0.41	52.18	0.28	61.45	0.15
Woodland/shrubland	44.64	0.39	56.05	0.17	51.88	0.22
2020						
Agriculture	29.13	0.55	44.15	0.28	44.15	0.30
Barren	26.42	0.60	33.67	0.58	29.56	0.66
Disturbed	--------	---------	26.42	0.65	36.07	0.54
Forest	74.51	0.09	44.15	0.43	35.65	0.57
Grasslands	73.54	0.13	51.78	0.35	44.29	0.45
Shrublands	78.01	0.08	84.76	0.08	80.83	0.10
Unassigned	89.72	0.06	68.98	0.20	56.07	0.35
Urban	33.08	0.58	51.98	0.25	75.96	0.09
Water	55.63	0.31	34.66	0.59	30.06	0.62
Wetland	40.67	0.44	48.15	0.43	49.44	0.38
Woodland/shrubland	82.16	0.10	76.71	0.14	76.55	0.12

Table 3.8. The effect of land use categories on six butterfly community traits at a spatial scale of 0.5 km in north-central Oklahoma using a fourth-corner analysis. Spatial scales 1 km and 1.5 km are reported in the supplementary section as Tables S6 and S7 respectively. There was no disturbed habitat at a spatial scale of 0.5 km. Values are presented as *r* (correlation coefficient), *p*.

2019

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	-0.027	0.874	-0.019	0.876	-0.013	0.937	0.052	0.504	-0.016	1.000	-0.030	0.821
Barren	-0.074	0.570	0.036	0.736	0.107	0.340	0.169	0.298	0.108	0.312	0.128	0.331
Forest	0.069	0.753	0.007	0.945	-0.127	0.529	-0.211	0.230	-0.117	0.512	-0.203	0.294
Grasslands	-0.079	0.730	-0.001	1.000	0.151	0.443	0.229	0.204	0.141	0.444	0.218	0.259
Shrublands	0.0987	0.643	0.000	0.951	-0.142	0.467	-0.244	0.161	-0.133	0.457	-0.199	0.316
Unassigned	0.0936	0.656	0.002	0.961	-0.138	0.462	-0.233	0.173	-0.129	0.461	-0.195	0.312
Urban	-0.004	0.985	-0.020	0.849	-0.047	0.690	-0.039	0.814	-0.049	0.640	-0.075	0.596
Water	-0.0265	0.893	-0.036	0.661	0.185	0.162	0.214	0.074	0.165	0.220	0.172	0.217
Wetland	-0.0284	0.942	-0.018	0.881	-0.012	0.952	0.052	0.624	-0.015	0.952	-0.030	0.731
Woodland/shrubland	0.0908	0.657	0.011	0.891	-0.162	0.385	-0.256	0.120	-0.149	0.399	-0.201	0.301

2020

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	0.027	0.853	-0.048	0.547	-0.063	0.405	-0.104	0.169	-0.070	0.496	-0.052	0.611
Barren	-0.081	0.503	0.044	0.699	0.023	0.888	0.095	0.371	0.032	0.81	-0.030	0.834
Forest	-0.090	0.578	-0.048	0.636	-0.083	0.722	-0.070	0.607	-0.088	0.678	-0.067	0.712
Grasslands	0.056	0.727	0.046	0.695	0.060	0.799	0.089	0.545	0.067	0.755	0.054	0.770
Shrublands	-0.057	0.723	-0.023	0.882	-0.027	0.924	-0.052	0.687	-0.030	0.908	-0.017	0.924
Unassigned	-0.064	0.692	-0.023	0.881	-0.029	0.914	-0.052	0.679	-0.032	0.888	-0.023	0.897
Urban	0.052	0.601	-0.068	0.407	-0.082	0.505	-0.107	0.127	-0.092	0.466	-0.042	0.580
Water	-0.100	0.517	0.008	0.991	-0.078	0.606	0.055	0.664	-0.069	0.676	0.024	0.883
Wetland	0.025	0.789	-0.049	0.524	-0.065	0.359	-0.104	0.108	-0.072	0.359	-0.053	0.353
Woodland/shrubland	-0.024	0.919	-0.012	0.985	0.010	0.924	-0.045	0.705	0.006	0.941	-0.012	0.943

Figures

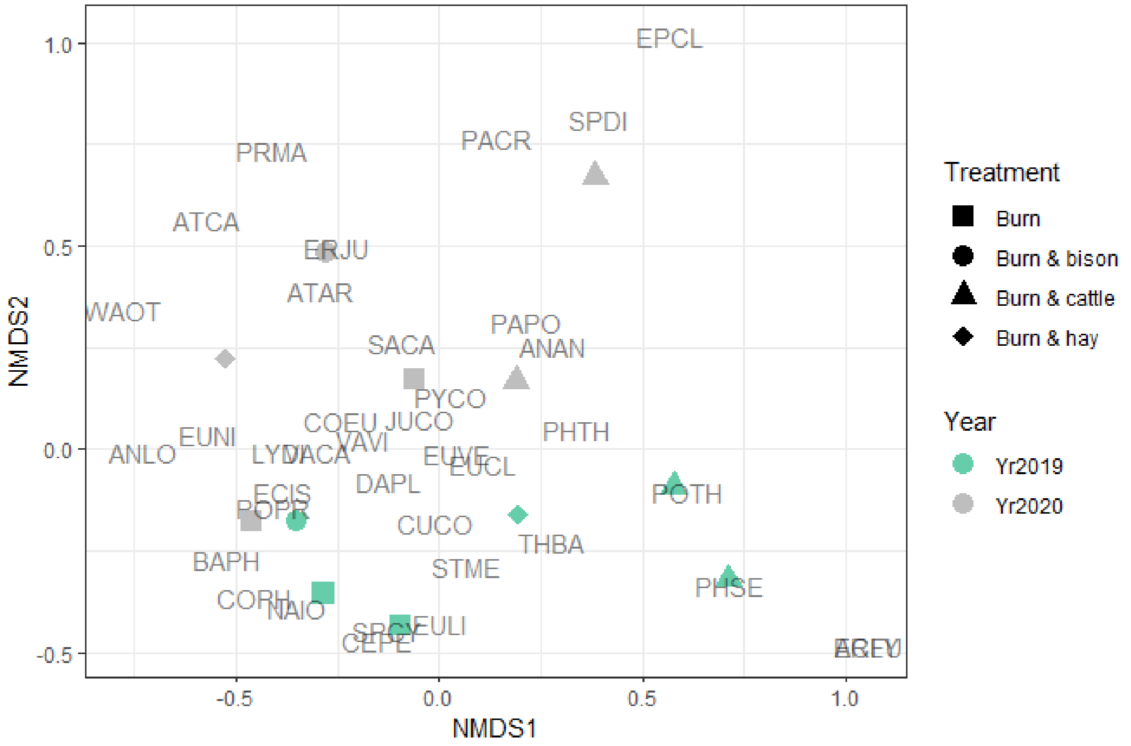

Figure 3.1. Non-metric dimensional scaling ordination diagram of management treatment types and the butterfly community. Shapes indicate type of treatment and colors indicate year of sampling. Butterfly species are represented by 4-letter codes. ACLY= *Achalarus lyciades*, ANAN= *Anaea andria*, ANLO= *Anatrytone logan*, ATAR= *Atrytone arogos*, ATCA= *Atalopedes campestris*, BAPH= *Battus philenor*, CEPE= *Cercyonis pegala*, COPH= *Colias philodice*, CUCO= *Cupido comyntas*, DAPL= *Danaus plexippus*, ECIS= *Echinargus isola*, EPCL= *Epargyreus clarus*, ERFU= *Erynnis funeralis*, ERJU= *Erynnis juvenalis*, EUCL= *Euptoieta claudia*, EULI= *Eurema lisa*, EUNI= *Eurema nicippe*, EUVE= *Euphyes vestris*, JUCO= *Junonia coenia*, LYDI= *Lycaena dione*, NAIO= *Nathalis iole*, PACR= *Papilio cresphontes*, PAPO= *Papilio polyxenes*, PHSE= *Phoebis sennae*, PHTH= *Phyciodes tharos*, POPR= *Pontia protodice*, POTH= *Polites themistocles*, PRMA= *Protographium marcellus*, PYCO= *Prygus communis*, SACA= *Satyrium calanus*, SPCY= *Speyeria cybele*, SPDI= *Speyeria diana*, STME= *Strymon melinus*, THBA= *Thorybes bathyllus*, VACA= *Vanessa cardui*, VAVI= *Vanessa virginiensis*, WAOT= *Wallengrenia otho*, ZECE= *Zerene cesonia.* The closer a butterfly species is to a shape the more abundant it was in sites that underwent that treatment.

CHAPTER IV

ENVIRONMENTAL VARIABLES INFLUENCING FIVE *SPEYERIA* (LEPIDOPTERA: NYMPHALIDAE) SPECIES' POTENTIAL DISTRIBUTIONS OF SUITABLE HABITAT IN THE EASTERN UNITED STATES

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Abstract

Five closely related species of greater fritillaries occur in North America east of the Mississippi River: regal fritillary (*Speyeria idalia* Drury [Lepidoptera: Nymphalidae]), Diana fritillary (*Speyeria diana* Cramer [Lepidoptera: Nymphalidae]), great spangled fritillary (*Speyeria cybele* Fabricius [Lepidoptera: Nymphalidae]), Atlantis fritillary (*Speyeria atlantis* Edwards [Lepidoptera: Nymphalidae]), and Aphrodite fritillary

(*Speyeria aphrodite* Fabricius [Lepidoptera: Nymphalidae]). The regal fritillary and Diana fritillary are species of concern whereas the great spangled fritillary, Atlantis fritillary, and Aphrodite fritillary are relatively abundant within their respective ranges. However, the Atlantis fritillary and Aphrodite fritillary have experienced severe population declines within the last few decades. We created ecological niche models for these five species by combining each species' known occurrences with climate and environmental variables to identify important response variables and determine the potential distribution of suitable habitat for each species. Important climate variables differed among species, although minimum temperature of the coldest month was important for great spangled, Atlantis, and Aphrodite fritillaries. The regal fritillary responded the most to temperature seasonality, whereas the Diana fritillary responded to maximum temperature of warmest month and the great spangled fritillary responded to annual precipitation. Land use was important for all species except the regal fritillary and average annual relative humidity was important for all species except the great spangled fritillary. This study highlights the different climate and habitat needs for greater fritillary species with important implications for how each species is expected to be impacted by climate change. We also demonstrate the value of citizen science and photo sharing websites for providing important data for evaluating species distributions.

Introduction

Butterflies have undergone declines across North America due to habitat loss, fragmentation, and degradation (Daniels et al. 2015). Within North America there are five closely related greater fritillary species (*Speyeria* spp.) east of the Mississippi River: the regal fritillary (*Speyeria idalia* Drury [Lepidoptera: Nymphalidae]), Diana fritillary (*Speyeria diana* Cramer [Lepidoptera: Nymphalidae]), great spangled fritillary (*Speyeria cybele* Fabricius [Lepidoptera: Nymphalidae]), Atlantis fritillary (*Speyeria atlantis* Edwards [Lepidoptera: Nymphalidae]), and Aphrodite fritillary (*Speyeria aphrodite* Fabricius [Lepidoptera: Nymphalidae]) (Hammond 1978, Campbell et al. 2007, Wells et al. 2011a, Caven et al. 2017). *Viola* spp. L. (Malpighiales: Violaceae) are the only hostplants for greater fritillary larvae (Hammond 1978, Scott 1986, Swengel and Swengel 2009). Violets senesce before females lay their eggs, so eggs are deposited indiscriminately in the surrounding litter (Baltosser 2007, Ferster and Vulinec 2010, Caven et al. 2017). First instars emerge and consume their egg chorion before entering diapause to overwinter (Wagner et al. 1997, Kopper et al. 2000, Baltosser 2007, Ferster and Vulinec 2010). In spring, the first instars leave diapause, go through five additional instars, pupate, and then emerge as adults 2–4 wk later (Hammond 1978, Baltosser 2007, Wagner et al. 1997, Ferster and Vulinec 2010). Sexes emerge asynchronously with females emerging approximately 1–2 wk after males (Hammond 1978, Carlton and Nobles 1996, Adams and Finkelstein 2006, James 2008, Ferster and Vulinec 2010, Wells et al. 2011a). Adults are nectar generalists and feed from a variety of plants including *Asclepias* spp. (Gentianales: Apocynaceae), *Monarda* spp. (Lamiales: Lamiaceae), and

Cirsium spp. (Asterales: Asteraceae) (Yahner 1998, Moran and Baldridge 2002, Rudolph et al. 2006, Baltosser 2007, Dunford 2009, Wells et al. 2011a).

Regal fritillaries and Diana fritillaries are of conservation concern due to declining populations and restricted habitat (Campbell et al. 2007, Wells et al. 2011a, 2011b, Wells and Smith 2013, Caven et al. 2017). In contrast, the great spangled fritillary, Atlantis fritillary, and Aphrodite fritillary are relatively abundant in the majority of their ranges (Rudolph et al. 2006;,Baltosser 2007; NatureServe 2018, 2020a, b). However, both the Atlantis fritillary and Aphrodite fritillary are imperiled at the edges of their respective ranges and both species have declined by 90% in portions of their eastern ranges in the past few decades (Breed et al. 2013; NatureServe 2020a,b).

The genus *Speyeria* consist of multiple species and subspecies across North America (Sims 2017). The genetic distance between *Speyeria* species is low suggesting less genetic change is necessary for speciation events to occur (Brittnacher et al. 1977, Baltosser 2007). The widespread distribution of this genus is most likely due to glacial maxima events that have occurred across North America throughout geological history, creating refugia and separating populations over time (Grey and Moeck 1962). Specifically, glacial patterns during the Pleistocene may account for the separation of the regal fritillary into two distinct subpopulations: an eastern and western subpopulation (Williams 2002, Powell et al. 2007, Selby 2007). These two subpopulations may be subspecies with the eastern population *S. idalia idalia* Drury, whereas the western population is a separate subspecies *S. idalia occidentalis* B. Williams (Selby 2007). In the late 1880s, regal fritillaries were a common species especially within the eastern portion of North America (Scudder 1889, Jones and Kimball 1943, Strichter 2015). By the late

1970s, occurrence records for the regal fritillary extended from southern Maine to parts of eastern Wyoming and Colorado, and as far south as northern Georgia (Hammond 1978). The range was revised by the mid 1980s with additional occurrence records extending to portions of New Brunswick and Nova Scotia in southern Canada with vagrants recorded as far northwest as Wyoming (Scott 1986). However, between the early 1980s and mid-1990s the eastern population underwent severe declines with only small disjunct populations remaining (Fernald 1884, Selby 2007). The cause of this decline is not known, but may be due to a variety of factors including habitat degradation, fragmentation, hurricanes, and land use change (Selby 2007, Chazal et al. 2010). The western subpopulation, which occurs west of the Mississippi River, now consists of multiple populations classified as vulnerable to critically imperiled, meaning populations are at a moderate to very high risk of extinction or elimination, respectively (Selby 2007).

Compared to regal fritillaries, Diana fritillaries have historically had a more restricted range (Hammond 1978). Diana fritillaries exist in two subpopulations that separated during the Last Glacial Maximum at least 20,000 yr ago (Wells et al. 2015). The two subpopulations of Diana fritillaries extended from the east coast to as far west as central Arkansas, north to central Ohio, and as far south as central Georgia in the 1970s (Hammond 1978, Baltosser 2007, Wells et al. 2018). Less than 10 yr later, occurrence records show a smaller range with the eastern extent of the range reaching West Virginia and extending only as far west as the northeastern corner of Arkansas (Scott 1986). No recent population distribution maps of Diana fritillaries exist, but since 1998, Diana fritillaries have been recorded along the eastern side of Oklahoma suggesting the species range has extended westward (Nelson and Fisher 2019; John Fisher, Unpublished data).

Great spangled fritillaries have historically had the broadest range of the five species. The range for great spangled fritillaries extended from the east to west coast, as far north as southern Canada and as far south as central Arkansas and Georgia in the late 1970s (Hammond 1978). The great spangled fritillary was recorded as far north as central Alberta by the late 1980s (Scott 1986). Great spangled fritillaries consist of at least two subspecies: a western subspecies (*Speyeria cybele leto* Behr) and an eastern subspecies (*Speyeria cybele cybele* Fabricius) with the subspecies separated by the Rocky Mountains (Hammond 1978). Similar to Diana fritillaries, no recent updates have been made to distribution maps for great spangled fritillaries.

The Atlantis fritillary is predominantly a more northern species with multiple disjunct populations (Dunford 2009, Swengel and Swengel 2009). Atlantis fritillaries have at least four distinct subspecies: *Speyeria atlantis atlantis* W. H. Edwards, *Speyeria atlantis hollandi* F. Chermock & R. Chermock, *Speyeria atlantis sorocko* Scott, Kondla & Spomer, and *Speyeria atlantis pahasapa* Spomer, Scott & Kondla (Dunford 2009). The *S. atlantis atlantis* range extends from as far west and south as Iowa and West Virginia, respectively, to as far northeast as portions of Newfoundland, Canada (Dunford 2009). The *S. a. hollandi* range extends Canada from Manitoba to British Columbia (Scott 1986, Dunford 2009). In comparison, both *S. a. sorocko* and *S. a. pahasapa* are restricted to the southern Rocky Mountains and portions of South Dakota, respectively (Dunford 2009). As with most of the *Speyeria* spp., the phylogenetics of the species is still being resolved and the Atlantis fritillary may have >20 subspecies (Campbell et al. 2020).

The Aphrodite fritillary has a broad range similar to the great spangled fritillary extending from Georgia to Nova Scotia and as far west as Washington (Scott 1986, Dunford 2009). However, the Aphrodite fritillary is a more northern species absent from much of the southern Great Plains and the southern west coast (Dunford 2009). Similar to the Atlantis fritillary, the Aphrodite fritillary has a number of disjunct populations and subspecies including *Speyeria aphrodite aphrodite* Fabricius, *Speyeria aphrodite byblis* W. Barnes & Benjamin, and *Speyeria aphrodite manitoba* F. Chermock & R. Chermock (Scott 1986). The potential distributions for both the Atlantis fritillary and Aphrodite fritillary have not been updated since the 1980s.

Potential distributions can be used to conserve and protect a species, such as locating areas where a species exists but is not documented, identifying areas to focus efforts on managing habitat, and estimating current distributions (Phillips et al. 2004a, Guisan et al. 2006). To develop potential distributions, an ecological niche is defined by combining a species' known occurrences with environmental variables (Phillips et al. 2004a). Potential distributions can be developed by Species Distribution Models (SDMs) that combine all potential geographical regions that fit a species' ecological niche (Phillips et al. 2004a). An SDM can show which environmental factors a species responds to within an environment (Miller 2010, Beane et al. 2013). This is useful for understudied species because SDMs can evaluate a species that has low occurrence records, exists in fragmented or difficult to access habitat, and needs quick assessments (Phillips et al. 2004a, Guisan et al. 2006, Miller 2010, Beane et al. 2013). SDMs can also be used to direct future sampling efforts and predict the effects of climate change (Lawler 2009, McCune 2016).

The objectives of this project were to use ecological niche models to 1) estimate the potential distribution of five greater fritillary species east of the Mississippi River and 2) identify the main climate and environmental response variables for each species.

Materials and Methods

Occupancy Data

Due to the complex phylogeny of greater fritillaries west of the Mississippi River, all occupancy data and model analysis were restricted to east of the Mississippi River to improve model accuracy. Occupancy records were found using citizen scientist websites that provide easy to access and free to use data: iNaturalist (http://iNaturalist.org), BugGuide (http://BugGuide.net), and Butterflies and Moth of North America (http://ButterfliesandMoths.org) and photo sharing websites Instagram (http://Instagram.com) and Flickr (http://Flickr.com). All entries were restricted to 1 January 2000 to 5 December 2018 to match available data across all websites. Because of the large number (>3,000) and even coverage of records for great spangled fritillaries on iNaturalist, only iNaturalist data were used for this species (Peterson 2001). Due to low regal fritillary numbers in the eastern United States, historic occurrence records from museums were added to increase occupancy data.

iNaturalist allows users to submit photos, which are reviewed by the iNaturalist community and identified to species (iNaturalist 2018). Three people out of the community view the photo and after two-thirds agree on an identification, the photo receives a species tag with high-quality records receiving ‘research grade’ status (iNaturalist 2018). Uploaded photos are stored in an Exchangeable Image File (EXIF) format with coordinates included among ancillary tags such as date and time. Coordinates are then included with iNaturalist records upon download. BugGuide specializes in invertebrate identification and has photo galleries of user submitted images (ISU 2018). Images are not associated with coordinates or maps, so we only used submissions with detailed locations (e.g., Cowboy trail, North West of Wood Lake, Cherry County, Nebraska) that allowed an approximate location with coordinates to be estimated on Google Maps. Accuracy (measurement close to value) in point placement is more important than precision (measurement close to one another) since modeling software can be robust to location errors up to 5 km (Graham et al. 2008). Anyone can upload sightings, photos, specimens, and historical museum records for any lepidopteran species to Butterflies and Moths of North America (Lotts and Naberhaus 2017). We only used records with photos or verified specimens. Similar to iNaturalist, coordinates are included with records.

Photo sharing sites require key word searches and we used various combinations of the terms: *Speyeria*, *idalia*, *diana*(s), regal(s), Atlantis, Aphrodite, fritillary(ies), butterfly(ies). Neither Instagram nor Flickr provide coordinates with user submitted photos. Instead, users have the option to include locations with their photos (either manually entering locations or using existing EXIF photo tags) and the websites will then geotag the images. Using these geotagged images, approximate locations can be identified and coordinates recorded. All photos were checked for duplicate entries (users may upload multiple photos of the same individual butterfly) and species accuracy. Regal fritillaries had few misidentifications, but Diana fritillaries had multiple misidentifications. Red-spotted purples (*Limenitis arthemis* Drury; Lepidoptera:

Nymphalidae), Pipevine swallowtails (*Battus philenor* L.; Lepidoptera: Nymphalidae), or Black swallowtails (*Papilio polyxenes* Fabricius; Lepidoptera: Nymphalidae) were most often confused for female Diana fritillaries. Variegated fritillaries (*Euptoieta claudia* Cramer; Lepidoptera: Nymphalidae) or great spangled fritillaries were frequently mistaken for male Diana fritillaries. Atlantis fritillaries were often confused for Aphrodite fritillaries and great spangled fritillaries. Similarly, Aphrodite fritillaries were commonly mistaken for Atlantis fritillaries and great spangled fritillaries. Due to high rates of misidentification for Atlantis fritillaries and Aphrodite fritillaries on photo-sharing websites, only citizen scientist websites were used for these two species.

In total, 175 records were found for regal fritillaries and after removing unusable records (those with no dates or locations), 109 remained and were used for analysis (Table 1). For Diana fritillaries, 384 records were located and after removing misidentifications and unusable records, 376 records remained (Table 1). After removing 59 great spangled fritillary records due to missing data, 3,005 records remained (Table 1). Finally, 1,026 and 1,258 records remained for Atlantis fritillaries and Aphrodite fritillaries after removing 30 and 32 records due to missing data, respectively (Table 1).

Occurrence records can be spatially autocorrelated due to bias in sampling areas, such as easily accessed locations or higher sampling efforts in urban areas (Radosavljevac and Anderson 2014). To reduce the effects of spatially autocorrelated points influencing the model, we rarefied records to 10 km using the SDMtoolbox 2.3 extension in ArcGIS (Radosavljevac and Anderson 2014, Brown et al. 2017). This left 38 records of regal fritillaries and 143 records of Diana fritillaries. Model overfitting continued to occur for great spangled fritillaries at 10 km, so we rarified records to 50 km leaving 274 records. For Atlantis fritillaries and Aphrodite fritillaries, records were rarified to 20 km to address model overfitting leaving 262 records and 302 records, respectively (Table 1).

Climate Variables

North America high-resolution (30 arc-s, 1 km) continuous BIOCLIM layers were downloaded from WorldClim version 2.0 (www.worldclim.org) for 19 bioclimatic variables (Fick and Hijmans 2017). To reduce collinearity, we chose climate variables by performing a principal components analysis (PCA) and choosing the variable that contributed the most information in three principal components (PCs) using R (Arellano et al. 2017, R Core Team 2020, version 3.3.2, R packages: sp, raster, maps, mapdata, RStoolbox). Three of the five species (regal fritillary, Diana fritillary, and Atlantis fritillary) had different sets of final climate variables, whereas the great spangled fritillary and Aphrodite fritillary had the same set of climate variables (Table 2).

Environmental Variables

Elevation, average annual relative humidity, average annual cumulative growing degree-days, and land use variables were also included in the models. Elevation can serve as a limiting factor for butterflies due to higher thermoregulatory stress and lower egg production experienced at higher elevations (Kingsolver and Watt 1983). Land use was included because each species has specific habitat preferences. Regal fritillaries are a grassland species that is sensitive to habitat fragmentation, whereas Diana fritillaries are a woodland species that occurs in old growth forest (Hammond 1978, Campbell et al. 2007, Caven et al. 2017). In contrast, great spangled fritillaries are a habitat generalist that frequents open grasslands (Swengel 2000, Vogel et al. 2007). Similarly, Atlantis fritillaries are restricted to meadow openings in forests while Aphrodite fritillaries are found in upland forest and prairie habitat (Swengel and Swengel 2009). These differences in habitat among the five species suggest that land use may be an important component to suitable habitat for each of the species.

Additionally, average annual relative humidity and average annual cumulative growing degree-day data were included. Humidity was included as it can determine egg success in Nymphalidae (Karlsson and Wiklund 1985, Clark and Faeth 1998). Cumulative growing degree-days were included because this information is commonly included in insect life cycle prediction (Lang et al. 2020). Including these additional variables can increase the accuracy of the final models.

For elevation data, we downloaded continuous 1-km scale data from USGS Earth explorer for the continental United States and Canada (USGS 2019). We merged these files into one raster using mosaic to raster within ESRI ArcMap 10.6.1. Categorical land use cover data were downloaded from USGS: The National Map Small Scale dataset (USGS 2018). Both average annual relative humidity and average annual cumulative growing degree-day data were downloaded from Atlas of the Biosphere (New et al. 1999; SAGE 2020a, b). We resampled land cover, humidity, and growing degree-day data to match climate and elevation data cell size. We used the mask to extent and raster to ASCII tools within ArcMap, so every variable had the same dimensions before use in a model (Young et al. 2011).

Model Processing

We used the software Maxent 3.4.1 to determine each species' maximum entropy distribution (Phillips et al. 2004b). Maxent uses presence data and creates pseudo-absences to find distribution patterns (Phillips et al. 2004b). We created polygons in ArcMap to define a study area encompassing all data points for each species. We projected the study area for each species to all of North America. Every model was run with a random 25% test, 15 subsampled replicates, and the maximum iterations increased to 5,000 to reach convergence (Young et al. 2011). We selected random seed so that every replicate's test dataset was independent (Beane et al. 2013). All other model settings were set to the default. All models had a jackknife run to find each variable's importance alone and its uniqueness when combined with other variables. Every species had 16 models run with different combinations of environmental variables (Table 3).

Postmodel Processing

Every model generates an area under the receiving curve (AUC) score which helps determine a model's goodness of fit (Phillips et al. 2004a, Vroh et al. 2016). Models with AUCs >0.7 are acceptable with higher scores indicating better model performance (Vroh et al. 2016; Table 3). The final model for each species was converted from ASCII back to raster in ArcMap. Maps were then converted into probability maps in 10% increments.

Results

Regal Fritillary

The final model included climate, elevation, average annual cumulative growing degree-days, and average annual relative humidity variables (model 14, AUC = 0.858), and showed potential regal fritillary habitat in the majority of the eastern United States as well as eastern Canada (Tables 2 and 3, Fig. 1). The variable with the highest importance and that contributed the most information to the model was elevation (40.9%) with the most important climate variable being temperature seasonality (BIO4; 18.7%; Table 4, Fig. 1; Supp Fig. 1 [online only]). Temperature seasonality is the difference between the minimum and maximum temperature in a year. Average annual cumulative growing degree-days (19.5%) contributed the most unique information to the model ranging from 0 to 4,830 d annually (Supp Fig. 2 [online only]). Average annual relative humidity provided 9.6% importance to the model with humidity ranging from 60 to 87% (Supp Fig. 3 [online only]).

Diana Fritillary

For Diana fritillaries, the final model included climate, land use, and average annual relative humidity variables (Model 7, AUC = 0.923; Tables 2 and 3). The final model depicted Diana fritillary habitat on the eastern side of the country aligning with previous range maps (Fig. 2). The variable that had the highest permutation importance in the model was maximum temperature of warmest month (BIO5; 51.5%; Table 5). This variable also had the highest gain when used by itself suggesting that maximum temperature of warmest month contained the most useful information when used in isolation. Additionally, this was the variable that decreased the most, which suggests that this variable provided the most unique information in the model. The model used to a lesser extent land use and average annual relative humidity variables (1.4 and 2.6% importance, respectively). The dominant land use type were evergreen needle-leaf forest, mixed forest, and deciduous broadleaf forest (Supp Fig. 4 [online only]). Average annual relative humidity ranged from 60 to 78% (Supp Fig. 5 [online only]).

Great Spangled Fritillary

The great spangled fritillary's final model included climate, land use, and elevation variables (Model 6, AUC = 0.890; Tables 2 and 3). The final model depicted great spangled fritillary habitat across the majority of the eastern United States with the exception of a band across the far southeast (Fig. 3). The variable that had the highest permutation importance in the model was elevation (41.6%) with the highest climate variable was annual precipitation (BIO12; 25.8%, Table 6, Supp Fig. 6 [online only]). This variable also had the highest gain when used by itself suggesting that annual precipitation contained the most useful information when used in isolation. Minimum temperature of the coldest month (BIO6; 23.5%) was the variable that decreased the most, which suggests that this variable provided the most unique information in the model. The model used land use variable to a lesser extent (6.3%). The dominant land use types was variable and ranged from evergreen needle-leaf forest and deciduous broadleaf forest to grassland/cropland mosaic (Supp Fig. 7 [online only]).

Atlantis Fritillary

For Atlantis fritillaries the final model included climate, land use, average annual cumulative growing degree-days, average annual relative humidity, and elevation variables (Model 16, AUC = 0.811; Tables 2 and 3). The final model depicted Atlantis fritillary habitat as the most northeastern of all the species (Fig. 4). The variable that had the highest permutation importance in the model was average annual cumulative growing degree-days (50.1%) and the highest climate variable was minimum temperature of coldest month (BIO6; 17.9%, Table 7; Supp Fig. 8 [online only]). Average annual cumulative growing degree-days had the highest gain when used by itself suggesting that average annual cumulative growing degree-days contained the most useful information when used in isolation. Average annual cumulative growing degree-days also decreased the most, which suggests this variable provided the most unique information in the model. The model used land use, average annual relative humidity, and elevation variables to a lesser extent (Table 7). The dominant land use type was forests including deciduous broadleaf forest and mixed forest (Supp Fig. 9 [online only]). Average annual relative humidity ranged from 60 to 83% (Supp Fig. 10 [online only]), and elevation ranged from −76 to 1,162 m above sea level (Supp Fig. 11 [online only]).

Aphrodite Fritillary

For Aphrodite fritillaries, the final model included climate, land use, average annual cumulative growing degree-days, and average annual relative humidity variables (Model 15, AUC = 0.755; Table 2 and 3). The final model depicted Aphrodite fritillary habitat on the eastern side of the country aligning with previous range maps with some suitable habitat identified in the southeastern United States (Fig. 5). The variable that had the highest permutation importance in the model was minimum temperature of the coldest month (BIO6; 44.4%; Table 8). Annual precipitation (BIO12; 13.5%) had the highest gain when used by itself suggesting that it contained the most useful information when used in isolation. Land use, average annual cumulative growing degree-days, and average annual relative humidity were used to a lesser extent (Table 8). The dominant land use type in the majority of the range was evergreen needle-leaf forest, mixed forest, and deciduous broadleaf forest (Supp Fig. 12 [online only]). In the northern portion of the range grassland and pasture were present as well. Average annual cumulative growing degree-days ranged from 977 to 3,709 (Supp Fig. 13 [online only]). Average annual relative humidity ranged from 60 to 83% (Supp. Fig. 14 [online only]).

Discussion

In this study, we present updated habitat suitability maps and main climate response variables for five greater fritillary species using SDM modeling. Four of the five species are undergoing population declines and SDM modeling allowed for rapid assessment and identification of climate and environmental variables that influence these species (Campbell et al. 2007, Miller 2010, Wells et al. 2011a, Beane et al. 2013, Breed et al. 2013). The suitable habitat area predictions generated by our models aligned with known historic distributions, although the habitat for regal fritillaries and Aphrodite fritillaries extended beyond known habitat boundaries. This could be due to limitations of the data used for the models. Although WorldClim data are used extensively in landscape and climate studies (Poggio et al. 2018), the data have known errors due to uneven distribution and availability of weather stations (Kumar 2012, Bedia et al. 2013).

Furthermore, because of the limited availability of information about each species' life history, suitable climatic variables were chosen by PCA rather than based on climate variables known to be important for each species (Kumar 2012). Some important climate variables may not have been included, as well as environmental variables that may influence the distribution of potential habitat, such as distance between populations or vegetation cover (Swengel and Swengel 2001). Additionally, information about the distribution of violets was not available to include in models, and the distribution of hostplants may be important for these species (Ries and Debinski 2001, Vogel et al. 2010). Finally, Maxent predicts suitable habitat envelopes based on climate and environmental factors (Lötters et al. 2010, Kumar 2012), and areas may be presented as suitable where a species will never occur, which should be considered when interpreting maps.

For regal fritillaries, suitable habitat covers the majority of the eastern United States and a large portion of eastern Canada. While the historic distribution of this species is represented within this range, there is far more suitable area compared with older range maps (Hammond 1978, Scott 1986, Ferster and Vulinec 2010). A potential reason for this is the lack of data on distance between populations and habitat boundaries, as it is likely regal fritillaries are responding to habitat fragmentation more so than the other four fritillary species and without these data suitable habitat predictions may be inflated (Ries and Debinski 2001, Powell et al. 2007, Keyghobadi et al. 2013). Furthermore, elevation contributed the most to the model with suitable habitat aligning with the Appalachian Mountains. As the model is using elevation more so than other factors, it may be potentially inflating suitable habitat. Interestingly, land use type was not included in the final model, despite regal fritillaries being habitat-specific prairie butterflies (Ries and Debinski 2001, Powell et al. 2007, Keyghobadi et al. 2013, Caven et al. 2017). As our land use variable only reflected dominant habitat rather than small patches and interstices, a finer scale land use raster potentially may reflect this land type requirement, as differing scales in land use studies and SDM modeling can produce different outcomes (de Koning et al. 1999, Changwan et al. 2009). Additionally, average annual cumulative growing degree-days and average annual relative humidity were both included in the final regal fritillary model. Cumulative growing degree-days can predict butterfly phenology (Cayton et al. 2015). Greater fritillaries have one generation a year with the sexes emerging asynchronously (Hammond 1978, Powell et al. 2007). As such, timing for life stages is crucial for this genus. The inclusion of cumulative growing degree days in the model may reflect this timing requirement. Finally, average annual relative humidity ranges were high, which may help prevent desiccation of regal fritillary eggs (Karlsson and Wiklund 1985, Clark and Faeth 1998), since eggs are laid in late summer/early fall when annual relative humidity decreases (Elliott and Angell 1997, Powell et al. 2007).

In comparison to the regal fritillary, the Diana fritillary potential distribution matched the historic distributions more closely with the Diana fritillary having the smallest amount of suitable habitat of all five species (Hammond 1978, Scott 1986). The Diana fritillary's known habitat consists predominantly of woodland and old growth forest, which dominate the southeastern United States and make up the majority of the range found in our models (Brown et al. 1999, Grell et al. 2005). However, logging of old growth forests has occurred prominently within this range (Hammond 1978, Campbell et al. 2007). The southeastern United States also has the second highest relative humidity among U.S. regions and this was reflected with average annual relative humidity in the Diana fritillary’s final model (Elliott and Angell 1997). However, both land use and relative humidity were less important to the Diana fritillary’s final model than climate variables.

In our models, great spangled fritillaries have the largest amount of suitable habitat in the United States of the five species. Additionally, great spangled fritillaries are highly vagile species with the second highest number of occurrence records after Aphrodite fritillaries, which may reflect their large range (Stasek et al. 2008). Similar to the regal fritillary, elevation was the most important variable in the model. Land use was used to a lesser extent but reflected the habitat generalist nature of great spangled fritillaries (Stasek et al. 2008). Great spangled fritillaries were the only one of the five species for which average annual relative humidity was not included in the final model.

The Atlantis fritillary had the most northern range of the five species with a large portion of eastern Canada potentially suitable for this species. The Atlantis fritillary was the only species for which every environmental variable was included in the final model and for which average annual cumulative growing degree-days was the most important. As with the regal fritillary, this may reflect issues with egg desiccation that influence distribution. Average annual relative humidity was the lowest and elevation the highest out of the five species likely due to the far northern range (Elliott and Angell 1997). Land use was predominantly forest, which matches the habitat requirements for this species (Dunford 2009).

Similar to the great spangled fritillary, the Aphrodite fritillary had a large range over the eastern United States and both included land use in the final model. However, the Aphrodite fritillary model also included average annual relative humidity and average annual cumulative growing degree-days, which was not included in the great spangled fritillary final model. Interestingly, suitable habitat was predicted in southeastern United States, where the Aphrodite fritillary has not been recorded (Scott 1986), but may reflect modeling constraints or unknown limiting factors for this species that were not accounted for in the models.

Despite sharing similar life histories and overlapping ranges, the greater fritillary species responded to a different suite of climate variables, with the exception of great spangled fritillaries and Aphrodite fritillaries. However, all five species include mean temperature of wettest quarter as an important climate variable. The three species with more northern documented occurrence records (great spangled fritillary, Atlantis fritillary, and Aphrodite fritillary) also included minimum temperature of coldest month as an important climate variable. Differences in climate variables suggest each species may be impacted differently by climate change.

Temperature seasonality was the main climate response variable for regal fritillaries, which means regal fritillaries are responding to the difference in temperature between summer and winter seasons (Andreasson and Schmitz 2000). As climate change increases the frequency of temperature extremes, regal fritillaries may be at risk from unpredictable weather patterns caused from this temperature variation as well as greater seasonality variation (Wuebbles and Hayhoe 2003, Vasseur et al. 2014).

For Diana fritillaries, the maximum temperature of the warmest month was the main response variable followed by temperature annual range. Temperature increases have the potential to alter insect phenology, migration, and range distribution (Walther et al. 2002, Vasseur et al. 2014). Additionally, climate models predict the southeastern United States as becoming hotter with wetter springs and drier summers/winters (Mearns et al. 2003). Our models match the historical records of Diana fritillaries having the most restricted range out of these five greater fritillary species (Hammond 1978, Scott 1986, Baltosser 2007). As butterflies shift their ranges northward in response to climate change our models suggest that further northward expansion for Diana fritillaries is not likely due to the lack of suitable habitat (Parmesan et al. 1999, Sparks et al. 2007). Climate change is already thought to be a potential cause of Diana fritillary range collapse as Diana fritillaries cannot shift their range northward as readily as other species (Wells and Tonkyn 2014). However, the western subpopulation of Diana fritillaries are being recorded in Oklahoma more frequently suggesting an ability to shift ranges westward may be possible (Nelson and Fisher 2019; John Fisher, Unpub. data). Climate change is increasing the occurrence of extreme weather events (e.g., freezing, flooding, and wildfires), which can contribute to mortality (Wells and Tonkyn 2014) and lead to the loss of small populations (Carlton and Nobles 1996, Wells et al. 2014). Consequently, Diana fritillaries may be at the greatest risk of population declines due to climate change of the five study species.

Our models indicate annual precipitation is the main climate response variable for great spangled fritillaries, followed by minimum temperature of coldest month. Larval success can be impacted by precipitation preventing larvae from feeding on host plant tissue (Kamata and Igarashi 1994). Additionally, McDermott Long et al. (2017) found that univoltine species experience detrimental effects at all life stages from extreme precipitation events. Extreme precipitation events are predicted in the northeast, which could increase the mortality of great spangled fritillaries at all life stages by washing eggs/larvae off hostplants and inundating pupae/adults (Rustad et al. 2012, Chen et al. 2019, McDermott Long et al. 2017). Although great spangled fritillaries have the largest range of the five species and use more habitat types, the species may still be negatively impacted by the effects of climate change if immature stages are negatively impacted (Stefanescu et al. 2010).

The main climate response variable for both the Atlantis fritillary and the Aphrodite fritillary was minimum temperature of the coldest month. All *Speyeria* spp. overwinter as first-instar larvae so freezing temperatures can cause mortality (Hammond 1978, Lee 1991). However, both the Atlantis fritillary and Aphrodite fritillary are cold-adapted species (Breed et al. 2013). Population trajectories developed by Breed et al. (2013), indicate both species continuing to decline in response to warming trends. Climate change will also contribute to more frequent freezes and ice storms moving further north and northeast, which comprises the majority of the Atlantis fritillary and Aphrodite fritillary ranges, respectively (Dale et al. 2001, Changnon and Changnon 2002, Wells et al. 2014). Cold-adapted insects use a variety of cold-hardiness techniques to survive winter but sudden freezes can still cause mortality (Lee 1989).

Additionally, climate change has the potential to impact violets. *Viola* spp. are a wide spread genus with early spring flowers and the majority of species pollinated by insects (Culley 2005). While not much is known about the ideal growing conditions of

Viola spp., plant phenology is predicted to shift with climate change, which could cause misalignment with necessary insect pollinators (Memmott et al. 2007). Furthermore, eggs are not laid directly on the hostplant, so all *Speyeria* spp. must find violets as larvae (Scott 1986, Powell et al. 2007). Any phenological delay or misalignment with the emergence of violets and larval timing could be detrimental to all *Speyeria* spp.

Conclusion

We present potential distributions for five greater fritillary species. Different climate and environmental variables were important for each species, suggesting they may be negatively affected by climate change in different ways and thus require different conservation strategies. Furthermore, as Speyeria spp. may have over 100 subspecies, further research on subspecies responses to climate and environmental variables is necessary to understand potential climate change impacts (Sims 2017). Additional research is needed to determine the distribution of hostplants to increase the accuracy of suitable habitat predictions, especially for regal fritillaries. As this study demonstrates, citizen science and photo sharing websites can provide important data for evaluating potential distributions of species of conservation concern.

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Figures

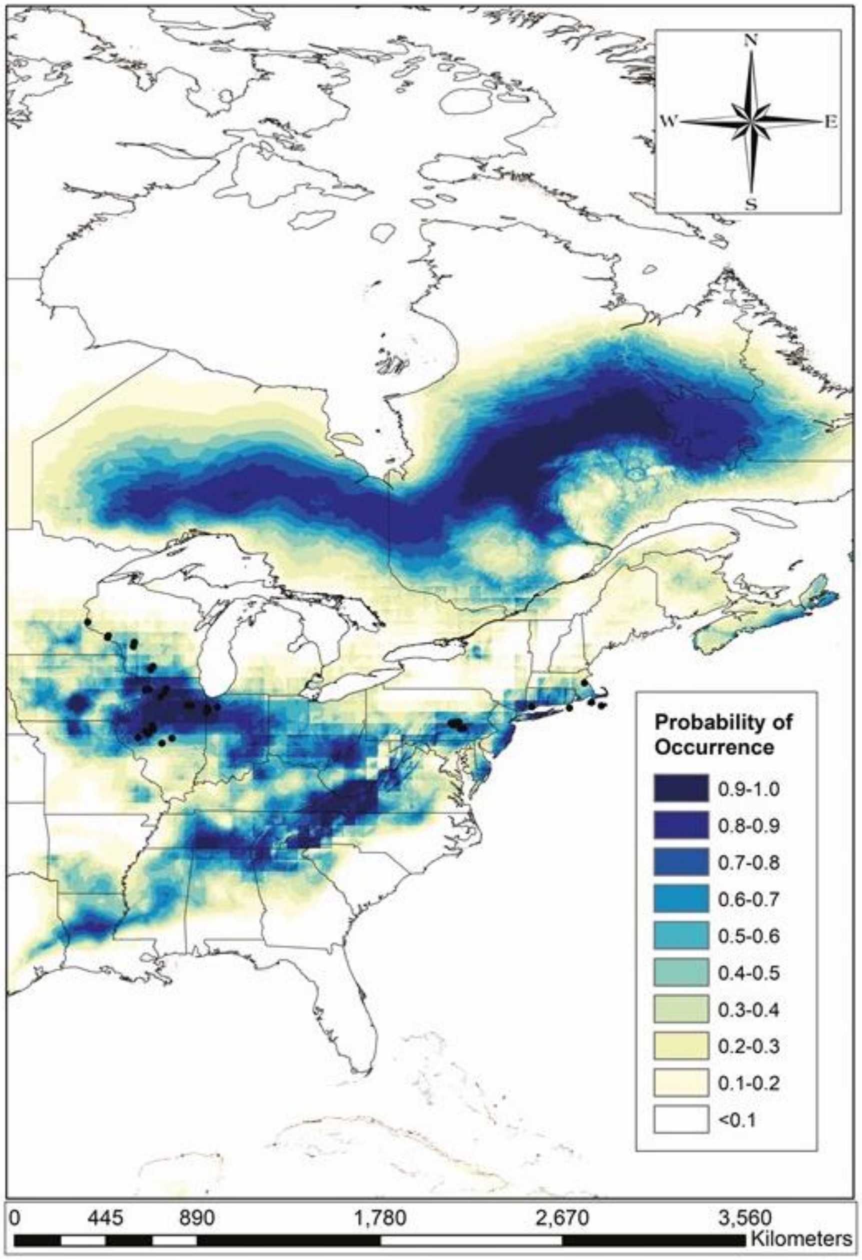

Fig. 4.1 Ecological niche model for regal fritillaries (*Speyeria idalia*) generated using climate and environmental variables. Probability of occurrence is displayed in 10% increments using a white (0% probability) to dark blue (100% probability) scale. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

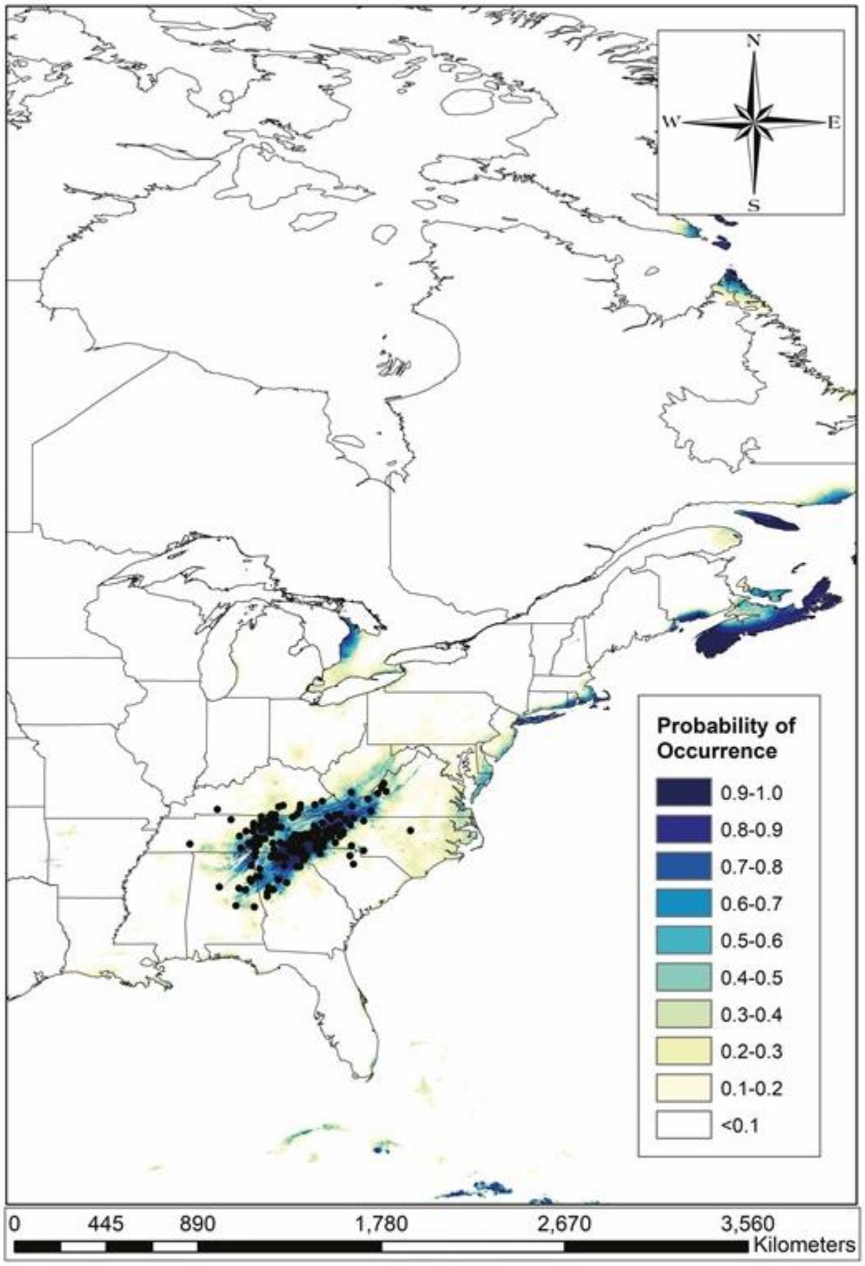

Fig.4.2 Ecological niche model for Diana fritillaries (*Speyeria diana*) generated using climate and environmental variables. Probability of occurrence is displayed in 10% increments using a white (0% probability) to dark blue (100% probability) scale. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

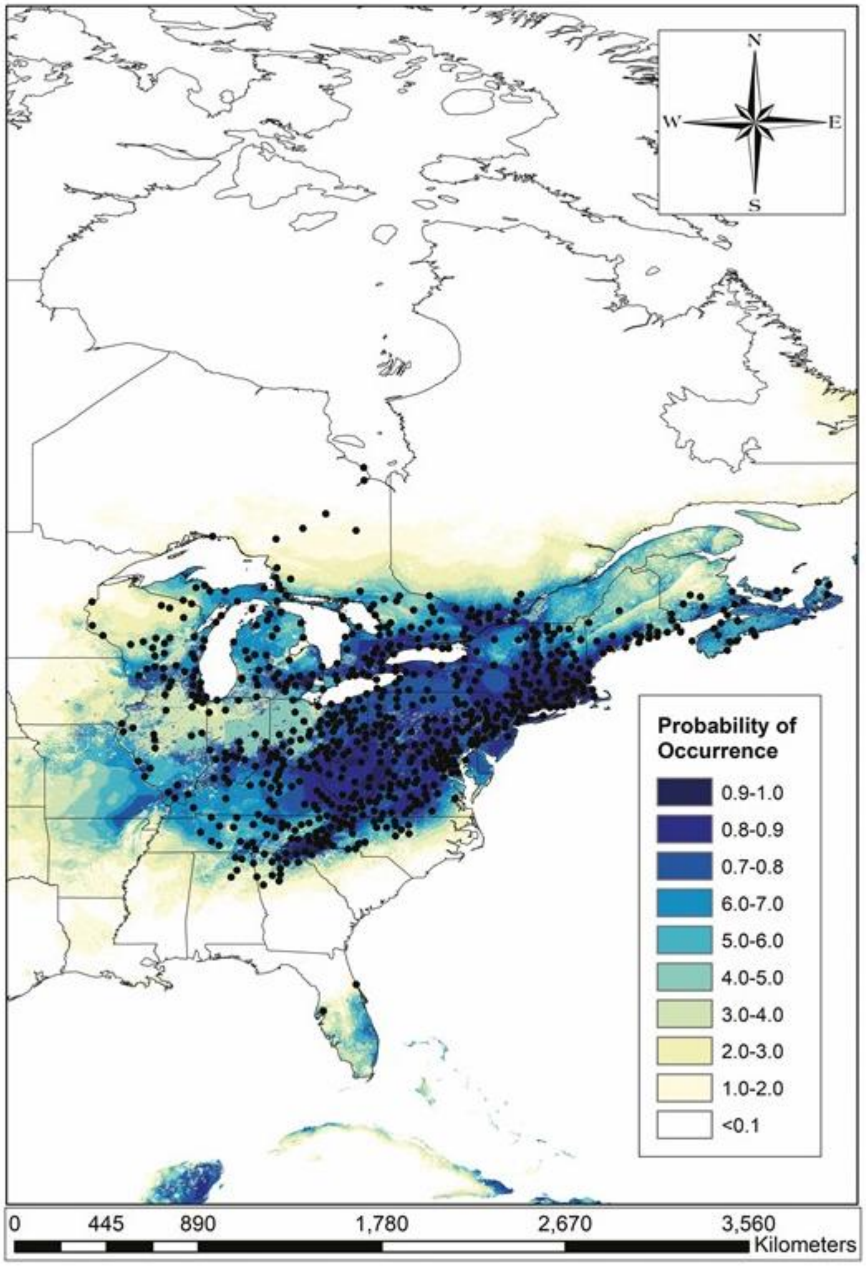

Fig. 4.3 Ecological niche model for great spangled fritillaries (*Speyeria cybele*) generated using climate and environmental variables. Probability of occurrence is displayed in 10% increments using a white (0% probability) to dark blue (100% probability) scale. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

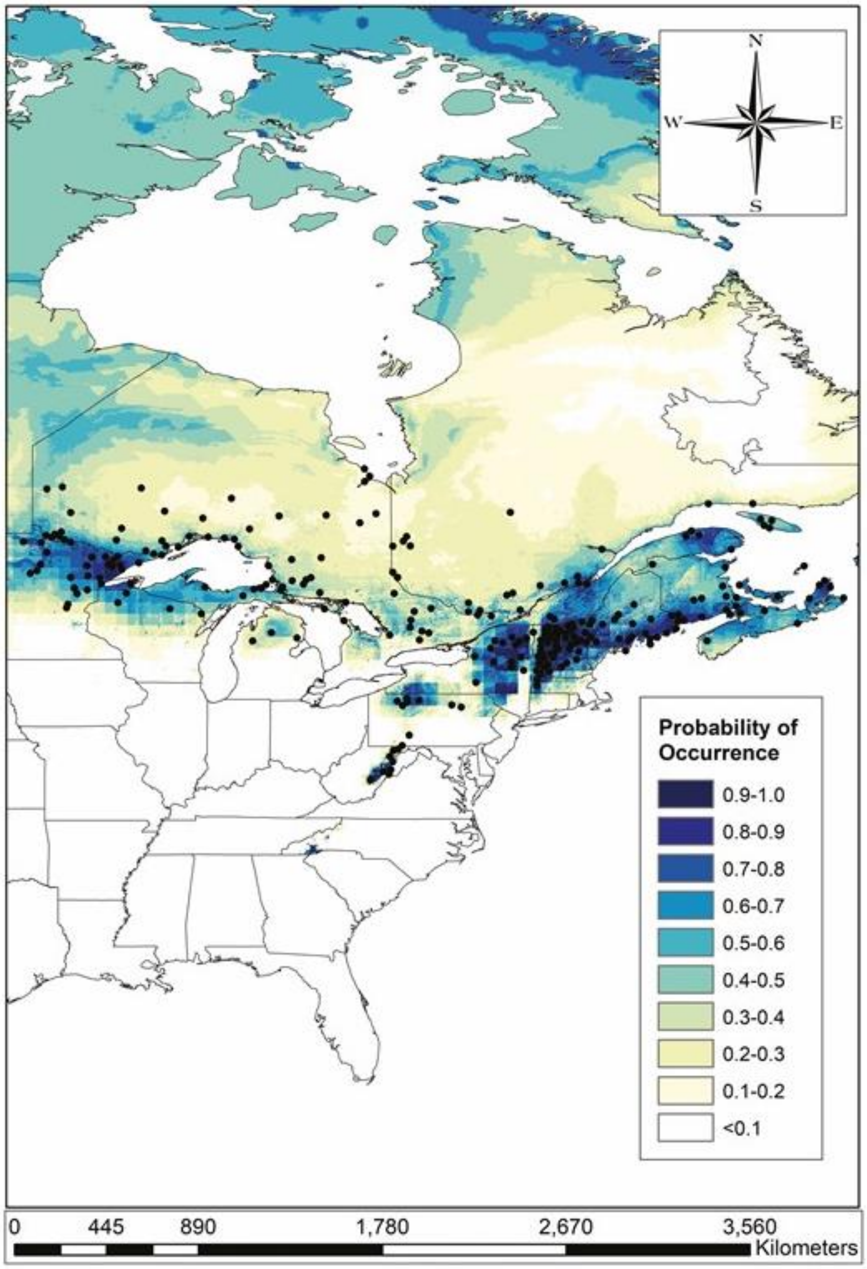

Fig. 4.4 Ecological niche model for Atlantis fritillaries (*Speyeria atlantis*) generated using climate and environmental variables. Probability of occurrence is displayed in 10% increments using a white (0% probability) to dark blue (100% probability) scale. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

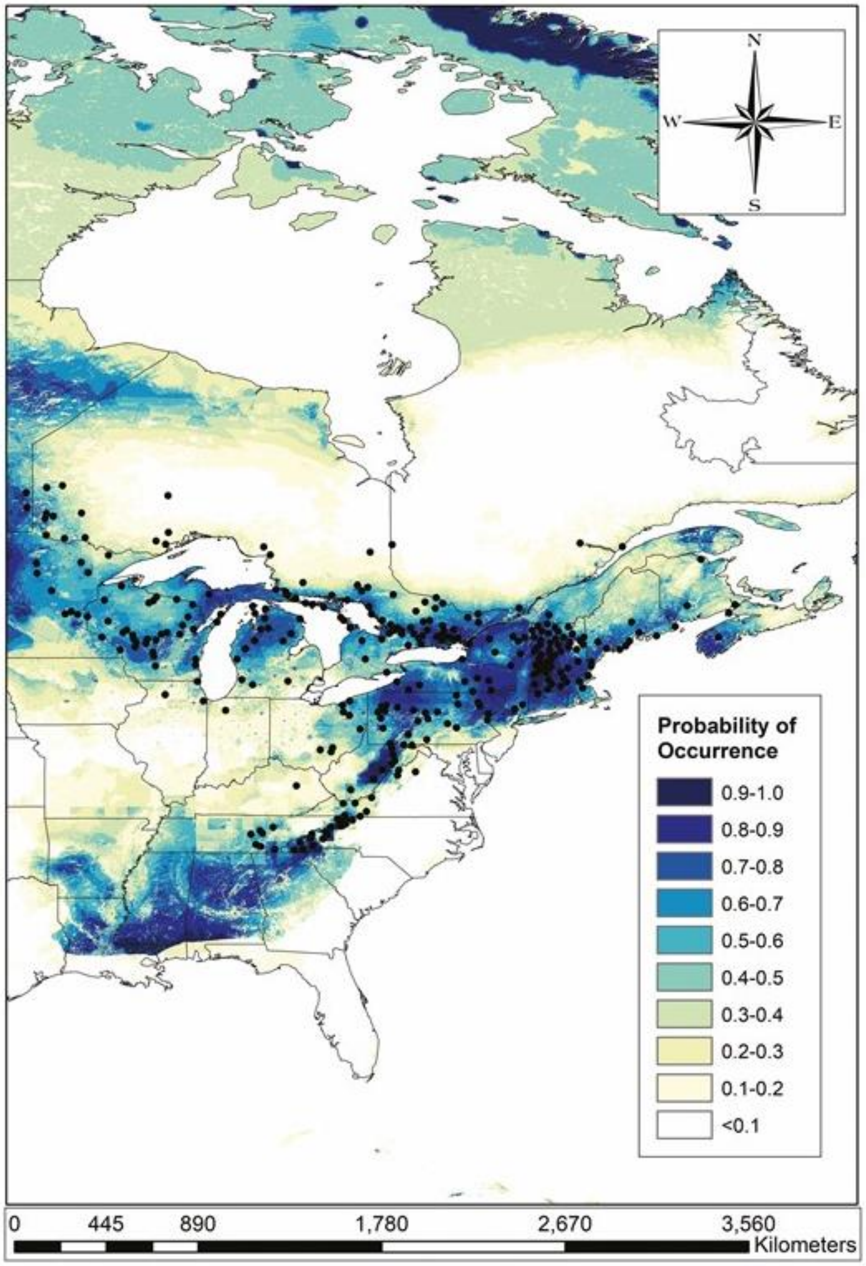

Fig. 4.5 Ecological niche model for Aphrodite fritillaries (*Speyeria aphrodite*) generated using climate and environmental variables. Probability of occurrence is displayed in 10% increments using a white (0% probability) to dark blue (100% probability) scale. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

Tables

Table 4.1 Total occurrence records found for five greater fritillary (*Speyeria* spp.) species east of the Mississippi River from citizen scientist projects and photo-sharing platforms. Only iNaturalist data were used for great spangled fritillaries (*Speyeria cybele*) due to the large number and even coverage of records for this species. Due to low numbers, historic records were included for regal fritillaries of recently extirpated populations. For Aphrodite fritillaries (*Speyeria aphrodite*) and Atlantis fritillaries (*Speyeria atlantis*), only citizen science platforms were used due to high rates of misidentification among photo-sharing platforms. Total relevant records (records east of the Mississippi River with complete information) are presented. To reduce spatial autocorrelation in models records were rarified. The total records used in each model after rarefication are presented.

Species	**iNaturalist**	**BugGuide**	**Butterflies and Moths of North America**	**Flickr**	**Instagram**	**Historic records**	**Total records (n)**	**Total relevant records (n)**	**Total records used in model (n)**
Aphrodite fritillary (*Speyeria aphrodite*)	455	6	829	-------	-------	-------	1290	1258	302
Atlantis fritillary (*Speyeria atlantis*)	604	4	448	-------	-------	-------	1056	1026	262
Diana fritillary (*Speyeria diana*)	93	5	268	15	3	-------	384	376	143
Great spangled fritillary (*Speyeria cybele*)	3064	-------	-------	-------	-------	-------	3064	3005	274
Regal fritillary (*Speyeria idalia*)	103	4	50	30	-------	18	175	109	38

Table 4.2 WorldClim climatic data were used in ecological niche models for five greater fritillary (*Speyeria* spp.) species. Final climate variables (out of 19 total) were determined by running a Principal Components Analysis (PCA), and choosing variables that contributed the most to the first three components. Final environmental variables were chosen by running 16 models and choosing models with the highest Area Under the Receiving Curve (Table 3).

Final model variables	**Aphrodite fritillary** (*Speyeria aphrodite*)	**Atlantis fritillary** (*Speyeria atlantis*)	**Diana fritillary** (*Speyeria diana*)	**Great spangled fritillary** (*Speyeria cybele*)	**Regal fritillary** (*Speyeria idalia*)
Climate variables					
Temp. Seasonality (4)					X
Max. Temp. of Warmest Month (5)			X		
Min. Temp. of Coldest Month (6)	X	X		X	
Temp. Annual Range (7)			X		
Mean Temp. of Wettest Quarter (8)	X	X	X	X	X
Annual Precipitation (12)	X			X	
Precipitation of Warmest Quarter (18)		X			X
Environmental variables					
Elevation		X		X	X
Average annual cumulative growing degree-days	X	X			X
Land use	X	X	X	X	
Average annual relative humidity	X	X	X		X

Table 4.3 Sixteen ecological niche models were run for five species of greater fritillary (*Speyeria* spp.). Variables used for each model and Area Under the Receiving Curve (AUC) score for each model are presented. Top models for each species are bolded.

Model number	**Model variables**	**Aphrodite fritillary** (*Speyeria aphrodite*)	**Atlantis fritillary** (*Speyeria atlantis*)	**Diana fritillary** (*Speyeria diana*)	**Great spangled fritillary** (*Speyeria cybele*)	**Regal fritillary** (*Speyeria idalia*)
1	Climate	0.736	0.767	0.913	0.853	0.772
2	Climate and elevation	0.732	0.788	0.907	0.884	0.813
3	Climate and land use	0.750	0.769	0.906	0.868	0.730
4	Climate and growing degree-days	0.717	0.783	0.907	0.883	0.807
5	Climate and relative humidity	0.734	0.782	0.907	0.864	0.774
6	Climate, land use, and elevation	0.747	0.803	0.903	**0.890**	0.781
7	Climate, land use, and relative humidity	0.744	0.797	**0.923**	0.879	0.748
8	Climate, land use, and growing degree-days	0.744	0.801	0.908	0.889	0.807
9	Climate, elevation, and relative humidity	0.738	0.799	0.905	0.656	0.811
10	Climate, elevation, and growing degree-days	0.723	0.792	0.908	0.884	0.847
11	Climate, relative humidity, and growing degree-days	0.740	0.794	0.905	0.885	0.846
12	Climate, elevation, land use, and growing degree-days	0.752	0.801	0.905	0.886	0.852
13	Climate, elevation, land use, and relative humidity	0.753	0.794	0.910	0.888	0.801
14	Climate, elevation, growing degree-days, and relative humidity	0.747	0.806	0.914	0.888	**0.858**
15	Climate, land use, growing degree-days, and relative humidity	**0.755**	0.801	0.906	0.881	0.807
16	Climate, land use, growing degree-days, relative humidity, and elevation	0.749	**0.811**	0.906	0.697	0.827

Table 4.4 The ecological niche model with the highest Area Under the Receiving Curve (AUC) score for the regal fritillary (*Speyeria idalia*) was model 14 (climate, elevation, growing degree-days, average annual relative humidity) with a AUC of 0.858. The permutation importance for each variable is presented.

Variable	**Model 14 Permutation importance %**
Climate variables	
Temp. Seasonality (4)	18.7
Mean Temp. of Wettest Quarter (8)	1.7
Precipitation of Warmest Quarter (18)	9.6
Environmental variables	
Average annual relative humidity	9.6
Average annual cumulative growing degree-days	19.5
Elevation	40.9
Land use	Not used

Table 4.5 The ecological niche model with the highest Area Under the Receiving Curve (AUC) score for the Diana fritillary (*Speyeria diana*) was model 7 (climate, land use, average annual relative humidity) with the AUC of 0.923. The permutation importance for each variable is presented.

Variable	**Model 7** **Permutation importance %**
Climate variables	
Max. Temp. of Warmest Month (5)	51.5
Temp. Annual Range (7)	41.2
Mean Temp. of Wettest Quarter (8)	2.6
Environmental variables	
Average annual relative humidity	2.6
Average annual cumulative growing degree-days	Not used
Elevation	Not used
Land use	1.4

Table 4.6 The ecological niche model with the highest Area Under the Receiving Curve (AUC) score for the great spangled fritillary (*Speyeria cybele*) was model 6 (climate, land use, elevation) with an AUC score of 0.890. The permutation importance for each variable is presented.

Variable	**Model 6 Permutation importance %**
Climate variables	
Min. Temp. of Coldest Month (6)	23.5
Mean Temp. of Wettest Quarter (8)	2.8
Annual Precipitation (12)	25.8
Environmental variables	
Average annual relative humidity	Not used
Average annual cumulative growing degree-days	Not used
Elevation	41.6
Land use	6.3

Table 4.7 The ecological niche model with the highest Area Under the Receiving Curve (AUC) score for the Atlantis fritillary (*Speyeria atlantis*) was model 16 (climate, land use, growing degree-days, average annual relative humidity, elevation) with an AUC score of 0.811. The permutation importance for each variable is presented.

Variable	**Model 16 Permutation importance %**
Climate variables	
Min. Temp. of Coldest Month (6)	17.9
Mean Temp. of Wettest Quarter (8)	2.6
Precipitation of Warmest Quarter (18)	3.5
Environmental variables	
Average annual relative humidity	8.8
Average annual cumulative growing degree-days	50.1
Elevation	10.6
Land use	6.5

Table 4.8 The ecological niche model with the highest Area Under the Receiving Curve (AUC) score for the Aphrodite fritillary (*Speyeria aphrodite*) was model 15 (climate, land use, growing degree-days, average annual relative humidity) with an AUC score of 0.755. The permutation importance for each variable is presented.

Variable	**Model 15 Permutation importance %**
Climate variables	
Min. Temp. of Coldest Month (6)	44.4
Mean Temp. of Wettest Quarter (8)	8.6
Annual Precipitation (12)	13.5
Environmental variables	
Average annual relative humidity	4.3
Average annual cumulative growing degree-days	19.9
Elevation	Not used
Land use	9.4

CHAPTER V

CONCLUSION

Managing for the butterfly community is complex and means managing for certain species over others as a single treatment is not effective for all species (Schlicht and Orwig 1990; Schultz and Crone 1998; Swengel 1998; Vogel et al. 2007). Patch-burn grazing may be an effective alternative, as it creates a mosaic of successional vegetation stages with different times since fire and grazing (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Swengel and Swengel 2007). Further research on role of timing of fire in regards to the presence of life stages can help provide context to the impacts of fire on different species.

However, patch-burn grazing is only one type of management that occurs in the Southern Great Plains. To evaluate multiple management methods on a consistent scale a modified Blüthgen et al. (2012) LUI equation is useful, but further research is needed on the effects of management timing and grazing timing on the butterfly community to refine the equation further. Combining LUI with a working knowledge of species natural histories can create a comparative ay to evaluate grassland butterflies across varied landscapes (Blüthgen et al. 2012, Börschig et al. 2013).

Finally, by using an ecological niche model approach for species of conservation concern, potential distributions, and response variables for grassland butterflies can be determined. Environmental and climate response variables can be used to understand how species may be affected by climate change differently and need differing conservation and management strategies. However, further research is needed on subspecies responses to fully understand potential climate change impacts. Additional research on incorporating hostplant distributions into models is necessary to increase accuracy of suitable habitat predictions.

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APPENDICES

APPENDIX A

Chapter III Supplementary Information

Supplementary Tables

Table A.1. Butterfly life history traits with individual trait descriptions, categorical codes, and data source used for information.

Trait	**Trait description**	**Data source**
Average wingspan	The average wingspan of a species determined by: $\text{Avg. WS} = \frac{\text{Min. WS} + \text{Max WS}}{2}$ Avg. WS = Average wingspan (cm) Min. WS = Minimum wingspan (cm) Max. WS = Maximum wingspan (cm)	Butterflies and Moth of North America (http://ButterfliesandMoths.org) Lotts and Naberhaus 2017
Voltinism	The number of generations per year (voltinism) in the southern United States. Categorical code 1 = univoltine (1 generation per year) 2 = bivoltine (2 generations per year) 3 = multivoltine (>2 generations a year)	Scott 1986 Brock and Kaufman 2003
Hostplant specialization	Total number of known hostplants in taxonomic families and genera represented as: Family (Genera). Hostplant specialist (S) or hostplant generalist (G) designation determined by: Hostplant genera ≤ 10 in 1 Family = *hostplant specialist* Hostplant genera > 10 in 1 Family = *hostplant generalist*	Scott 1986 Kitahara et al. 2000

	Hostplants in ≥ 2 Families = *hostplant generalist* Categorical code 1 = hostplant specialist 2 = hostplant generalist	
Hostplant category	Based on hostplants, each butterfly species was categorized as using grasses, forbs, trees, shrubs, or sedges. Categorical code 1 = Grasses 2 = Forbs 3 = Trees 4 = Forb and trees 5 = Trees and shrubs 6 = Sedges 7 = Forb/shrub	Scott 1986
Overall specialization	Butterflies were categorized as either true specialists, true generalists, or intermediate as determined by: Oligovoltine (1 or 2 generations) + hostplant specialist = *true specialist* Multivoltine (3+ generations) + hostplant generalist = *true generalist* Oligovoltine + hostplant generalist = *intermediate* Multivoltine + hostplant specialist = *intermediate* Categorical code 1: True specialist 2: Intermediate 3: True generalist	Kitahara et al. 2000
Overwintering stage	The life stage a species is in during winter. If a species migrates to a warmer area then it is listed as a migrant rather than by life stage.	Comstock 1940 Stamp 1980 Walker 1985 Scott 1986 Scott and Epstein 1987

	Categorical code 1: Egg 2: Larva 3: Larva or pupa 4: Pupa 5: Pupa or adult 6: Adult 7: Migrant	Schlicht and Orwig 1990 Schweitzer 2006 Bartel et al. 2011 Henry and Beyer 2013

Table A.2. Land use categories from the Oklahoma Department of Wildlife Conservation vegetation GIS raster combined into 11 broad landscape categories.

Broad category	Combined categories
Agriculture	Row crops
Barren	Barren, Riparian barren, Bottomland barren
Disturbed habitat	Disturbed soil pasture (i.e. non-native and/or disturbance tolerant species)
Forest	Cross Timbers post oak-blackjack oak forest and woodland, Cross Timbers sandyland post oak-blackjack oak forest and woodland, Cross Timbers young post oak-blackjack oak woodland, High Plains bottomland hardwood forest, High Plains riparian hardwood woodland, High Plains riparian mixed hardwood-eastern red cedar woodland, Ruderal deciduous woodland, Ruderal mixed deciduous eastern red cedar woodland, South Central Interior bottomland hardwood forest, South Central Interior riparian hardwood woodland
Grasslands	Mixed grass prairie/pasture, Cross timbers pasture/prairie, Flint Hills tallgrass prairie/pasture
Shrubland	Cross timbers sandyland shrubland and grassland, High Plains bottomland deciduous shrubland, High Plains riparian deciduous shrubland
Unassigned	Raster data that was unassigned a land type category
Urban	Urban low intensity
Water	Open water
Wetland	Eastern Great Plains herbaceous wetland, High Plains bottomland herbaceous wetland, High Plains riparian herbaceous wetland, South Central Interior riparian herbaceous wetland
Woodland-Shrubland mix	Cross timbers eastern red cedar woodland and shrubland, High Plains bottomland eastern red cedar woodland and shrubland, High Plains riparian eastern red cedar woodland and shrubland, Ruderal deciduous shrubland and young woodland, Ruderal eastern red cedar woodland and shrubland, South Central Interior bottomland shrubland and young woodland, South Central Interior riparian shrubland and young woodland

Table A.3. The average percentage of land use categories at three spatial scales at six sites in north-central Oklahoma. Sites: BU= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Bison Unit, JD =John Dahl Wildlife Management Area (WMA), KAW= Kaw WMA, NT= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Nature Trail Area, RCU= Osage WMA Rock Creek Unit, and WWU= Osage WMA Western Wall Unit. Agr. = Agriculture, Dist. = Disturbed habitat, Wood/Shrub= Woodland-Shrubland mix

	Average % land type 0.5km										
Site	Agr.	Barren	Dist.	Forest	Grasslands	Shrub.	Unassigned	Urban	Water	Wetland	Wood/Shrub
BU	0.00	0.00	0.00	0.00	94.45	0.00	0.00	1.62	0.00	0.00	3.93
JD	0.00	0.00	0.00	0.00	97.69	0.00	0.00	1.47	0.84	0.00	0.00
KAW	7.24	0.00	0.00	8.28	75.18	0.00	0.20	3.09	0.23	4.77	1.02
NT	0.00	0.00	0.00	20.97	50.51	6.62	3.09	1.35	0.00	0.00	17.46
RCU	0.00	0.00	0.00	9.51	86.99	0.00	0.00	2.69	0.52	0.14	0.14
WWU	0.00	0.23	0.00	5.20	93.08	0.00	0.34	0.00	0.96	0.00	0.18

	Average % land type 1.0km										
Site	Agr.	Barren	Dist.	Forest	Grasslands	Shrubland	Unassigned	Urban	Water	Wetland	Wood/Shrub
BU	0.00	0.00	0.00	2.08	93.47	0.16	0.00	0.90	0.36	0.05	2.99
JD	0.00	0.42	0.00	0.00	98.57	0.00	0.00	0.77	0.24	0.00	0.00
KAW	7.72	0.00	0.00	12.68	69.36	0.00	0.06	1.60	0.51	7.11	0.97
NT	0.00	0.34	0.00	10.22	74.19	2.61	3.86	1.05	0.49	0.19	7.06
RCU	0.00	0.00	1.12	8.38	88.60	0.00	0.06	1.04	0.18	0.38	0.23
WWU	0.00	0.58	0.00	10.57	86.22	0.09	1.61	0.00	0.74	0.09	0.10

	Average % land type 1.5km										
Site	Agr.	Barren	Dist.	Forest	Grasslands	Shrubland	Unassigned	Urban	Water	Wetland	Wood/Shrub
BU	0.00	0.00	0.00	2.39	93.41	0.57	0.02	0.71	0.37	0.05	2.49
JD	0.00	0.35	0.00	0.00	98.41	0.00	0.00	0.55	0.65	0.03	0.00
KAW	6.13	0.00	0.05	13.38	70.99	0.01	0.15	1.24	0.26	6.90	0.90
NT	0.00	0.15	0.00	8.66	77.55	2.07	3.37	1.75	0.45	0.18	5.84
RCU	0.00	0.00	0.69	11.45	85.24	0.00	0.05	1.59	0.11	0.33	0.55
WWU	0.00	0.28	0.00	17.42	77.80	0.05	3.46	0.00	0.36	0.35	0.28

Table A.4. Abundances of butterflies by species and total butterfly species seen in north-central Oklahoma in June 2019 and 2020. Six butterflies were unable to be identified to species in 2019.

Family & Species	Common name	2019	2020	Total
Hesperiidae				
Achalarus lyciades	Hoary edge	2	0	2
Anatrytone logan	Delaware skipper	0	2	2
Atalopedes campestris	Sachem	0	2	2
Atrytone arogos	Arogos skipper	4	21	25
Epargyreus clarus	Silver-spotted skipper	0	1	1
Erynnis funeralis	Funereal duskywing	1	0	1
Erynnis juvenalis	Juvenal's duskywing	0	3	3
Euphyes vestris	Dun skipper	2	2	4
Polites themistocles	Tawny-edged skipper	14	4	18
Pyrgus communis	Common checkered-skipper	4	5	9
Thorybes bathyllus	Southern cloudywing	3	6	9
Wallengrenia otho	Southern broken dash	0	2	2
Lycaenidae				
Echinargus isola	Reakirt’s blue	1	19	20
Everes comyntas	Eastern tailed-blue	148	111	259
Lycaena dione	Gray copper	0	3	3
Satyrium calanus	Banded hairstreak	0	1	1
Strymon melinus	Gray hairstreak	28	9	37
Nymphalidae				
Anaea andria	Goatweed leafwing	0	1	1
Cercyonis pegala	Common wood-nymph	33	3	36
Danaus plexippus	Monarch	39	50	89
Euptoieta claudia	Variegated fritillary	25	28	53
Junonia coenia	Common buckeye	16	50	66
Phyciodes tharos	Pearl crescent	10	23	33
Speyeria cybele	Great spangled fritillary	2	1	3
Speyeria diana	Diana fritillary	0	2	2
Vanessa cardui	Painted lady	3	6	9
Vanessa virginiensis	American lady	5	8	13
Papilionidae				
Battus philenor	Pipevine swallowtail	1	0	1
Papilio cresphontes	Giant swallowtail	1	5	6
Papilio polyxenes	Black swallowtail	10	20	30
Protographium marcellus	Zebra swallowtail	0	1	1
Pieridae				
Colias eurytheme	Orange sulphur	41	76	117
Colias philodice	Clouded sulphur	4	2	6

Eurema lisa	Little yellow	34	2	36
Eurema nicippe	Sleepy orange	2	3	5
Nathalis iole	Dainty sulphur	4	1	5
Phoebis sennae	Cloudless sulphur	3	0	3
Pontia protodice	Checkered white	11	11	22
Zerene cesonia	Southern dogface	0	1	0
Unknown		6	0	6
Total species		28	35	38
Total butterflies		451	485	935

Table A.5. List of butterfly species seen in north-central Oklahoma in June 2019 and 2020. Life history traits for each species are included (see **Table A.1** for trait descriptions). Avg. WS = average wingspan.

Family & Species	**Common name**	**Avg. WS (cm)**	**Voltinism**	**Hostplant specialization**	**Hostplant category**	**Overall specialization**	**Over-wintering stage**
Hesperiidae							
Achalarus lyciades	Hoary edge	4.7	Multi	Specialist	Forb	Intermediate	Pupa
Anatrytone logan	Delaware skipper	3.4	Bi	Specialist	Grass	Specialist	Larva
Atalopedes campestris	Sachem	3.7	Multi	Specialist	Grass	Intermediate	Migrant
Atrytone arogos	Arogos skipper	3.3	Multi	Specialist	Grass	Intermediate	Pupa
Epargyreus clarus	Silver-spotted skipper	5.6	Bi	Generalist	Forb/Tree	Intermediate	Pupa
Erynnis funeralis	Funereal duskywing	4.0	Multi	Specialist	Forb	Intermediate	Pupa
Erynnis juvenalis	Juvenal's duskywing	4.1	Bi	Specialist	Tree/shrub	Specialist	Larva
Euphyes vestris	Dun skipper	3.2	Multi	Specialist	Sedges	Intermediate	Pupa
Polites themistocles	Tawny-edged skipper	2.9	Multi	Specialist	Grass	Intermediate	Adult
Pyrgus communis	Common checkered-skipper	3.2	Multi	Generalist	Forb	Generalist	Pupa
Thorybes bathyllus	Southern cloudywing	4.2	Multi	Specialist	Forb	Intermediate	Pupa
Wallengrenia otho	Southern broken dash	3.0	Bi	Specialist	Grass	Specialist	Larva
Lycaenidae							
Echinargus isola	Reakirt’s blue	2.5	Multi	Generalist	Forb/shrub	Generalist	Migrant
Everes comyntas	Eastern tailed-blue	2.6	Multi	Generalist	Forb/shrub	Generalist	Pupa
Lycaena dione	Gray copper	3.1	Uni	Specialist	Forb	Specialist	Egg
Satyrium calanus	Banded hairstreak	3.2	Uni	Generalist	Forb	Intermediate	Egg
Strymon melinus	Gray hairstreak	2.9	Multi	Generalist	Forb/shrub	Generalist	Adult
Nymphalidae							
Anaea andria	Goatweed leafwing	7.1	Bi	Specialist	Tree	Specialist	Adult
Cercyonis pegala	Common wood-nymph	6.1	Uni	Specialist	Grass	Specialist	Pupa
Danaus plexippus	Monarch	10.5	Multi	Generalist	Forb	Generalist	Migrant
Euptoieta claudia	Variegated fritillary	6.3	Multi	Generalist	Forb	Generalist	Migrant
Junonia coenia	Common buckeye	5.6	Multi	Generalist	Forb	Generalist	Adult

Phyciodes tharos	Pearl crescent	3.9	Multi	Specialist	Forb	Intermediate	Pupa
Speyeria cybele	Great spangled fritillary	8.2	Uni	Specialist	Forb	Specialist	Pupa
Speyeria diana	Diana fritillary	10.0	Uni	Specialist	Forb	Specialist	Larva
Vanessa atalanta	Red admiral	6.1	Multi	Generalist	Forb	Generalist	Pupa or adult
Vanessa cardui	Painted lady	6.2	Multi	Generalist	Forb	Generalist	Pupa or adult
Vanessa virginiensis	American lady	5.6	Multi	Generalist	Forb	Generalist	Adult
Papilionidae							
Battus philenor	Pipevine swallowtail	10.0	Multi	Generalist	Forb/shrub	Generalist	Adult
Papilio cresphontes	Giant swallowtail	13.1	Multi	Generalist	Forb	Generalist	Adult
Papilio polyxenes	Black swallowtail	9.5	Multi	Generalist	Forb	Generalist	Adult
Protographium marcellus	Zebra swallowtail	8.4	Bi	Specialist	Tree	Specialist	Pupa
Pieridae							
Colias eurytheme	Orange sulphur	5.3	Multi	Generalist	Forb	Generalist	Larva or pupa
Colias philodice	Clouded sulphur	5.4	Multi	Generalist	Forb	Generalist	Larva or pupa
Eurema lisa	Little yellow	3.8	Multi	Specialist	Forb	Intermediate	Migrant
Eurema nicippe	Sleepy orange	4.6	Multi	Specialist	Forb	Intermediate	Migrant
Nathalis iole	Dainty sulphur	2.6	Multi	Generalist	Forb	Generalist	Migrant
Phoebis sennae	Cloudless sulphur	6.9	Multi	Generalist	Forb/shrub	Generalist	Migrant
Pontia protodice	Checkered white	5.1	Multi	Generalist	Forb	Generalist	Adult
Zerene cesonia	Southern dogface	6.5	Multi	Specialist	Forb	Intermediate	Adult

Table A.6. The effect of land use categories on six butterfly community traits at a spatial scale of 1.0 km in north-central Oklahoma using a fourth-corner analysis. Values are presented as *r* (correlation coefficient), *p*.

2019

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	0.051	0.687	-0.045	0.625	0.001	0.995	-0.031	0.731	0.052	0.692	0.051	0.687
Barren	-0.048	0.586	0.008	0.927	-0.112	0.578	-0.003	0.999	-0.073	0.712	-0.048	0.586
Disturbed	0.036	0.796	0.107	0.368	0.169	0.329	0.108	0.354	0.128	0.281	0.036	0.796
Forest	0.087	0.221	-0.097	0.332	-0.112	0.557	-0.072	0.519	-0.056	0.700	0.087	0.221
Grasslands	-0.069	0.390	0.142	0.216	0.168	0.219	0.118	0.322	0.098	0.427	-0.069	0.390
Shrublands	-0.001	0.985	-0.144	0.520	-0.245	0.157	-0.135	0.531	-0.203	0.318	-0.001	0.985
Unassigned	0.007	0.845	-0.133	0.599	-0.243	0.167	-0.123	0.582	-0.199	0.341	0.007	0.845
Urban	0.038	0.667	-0.081	0.417	-0.033	0.770	-0.067	0.459	0.009	0.967	0.038	0.667
Water	0.048	0.491	-0.119	0.468	-0.174	0.236	-0.101	0.504	-0.129	0.413	0.048	0.491
Wetland	0.053	0.644	-0.045	0.627	0.002	0.999	-0.030	0.730	0.052	0.721	0.053	0.644
Woodland/shrubland	0.001	0.985	-0.164	0.423	-0.241	0.150	-0.153	0.467	-0.219	0.265	0.001	0.985

2020

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	0.049	0.780	0.013	0.913	-0.020	0.962	0.054	0.604	-0.005	0.982	-0.003	0.977
Barren	-0.102	0.323	0.014	0.910	0.056	0.645	-0.074	0.419	0.031	0.759	-0.015	0.903
Disturbed	-0.100	0.308	0.003	0.999	0.104	0.464	0.029	0.806	0.068	0.291	0.008	0.901
Forest	-0.009	0.939	0.137	0.171	-0.045	0.718	0.118	0.268	0.039	0.722	0.161	0.116
Grasslands	-0.036	0.775	-0.108	0.324	0.066	0.641	-0.132	0.223	-0.010	0.933	-0.142	0.212
Shrublands	0.010	0.938	0.071	0.478	-0.049	0.656	0.090	0.396	-0.003	0.999	0.122	0.224
Unassigned	-0.009	0.971	0.094	0.329	-0.049	0.669	0.077	0.501	0.009	0.912	0.138	0.163
Urban	0.065	0.542	-0.018	0.887	-0.005	0.997	0.120	0.134	-0.014	0.882	0.007	0.948
Water	0.052	0.687	0.133	0.182	-0.131	0.331	0.030	0.869	-0.013	0.939	0.142	0.234
Wetland	0.046	0.790	0.016	0.888	-0.018	0.936	0.059	0.559	-0.002	0.998	0.002	0.971
Woodland/shrubland	0.065	0.566	0.068	0.524	-0.098	0.438	0.096	0.383	-0.030	0.824	0.131	0.239

Table A.7. The effect of land use categories on six butterfly community traits at a spatial scale of 1.5 km in north-central Oklahoma using a fourth-corner analysis. Values are presented as *r* (correlation coefficient), *p*.

2019

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	0.051	0.745	-0.045	0.633	0.001	0.962	-0.031	0.754	0.052	0.636	0.051	0.745
Barren	-0.070	0.271	0.055	0.649	-0.042	0.913	0.036	0.788	-0.009	0.969	-0.070	0.271
Disturbed	0.041	0.699	0.105	0.397	0.172	0.268	0.107	0.357	0.135	0.241	0.041	0.699
Forest	0.093	0.256	-0.038	0.724	-0.033	0.875	-0.015	0.860	0.002	0.984	0.093	0.256
Grasslands	-0.082	0.331	0.113	0.249	0.131	0.430	0.088	0.408	0.069	0.612	-0.082	0.331
Shrublands	-0.004	0.979	-0.151	0.441	-0.241	0.168	-0.142	0.474	-0.214	0.270	-0.004	0.979
Unassigned	0.016	0.747	-0.111	0.659	-0.223	0.166	-0.101	0.634	-0.183	0.329	0.016	0.747
Urban	0.041	0.547	-0.104	0.300	-0.122	0.445	-0.089	0.360	-0.085	0.534	0.041	0.547
Water	-0.090	0.329	-0.008	0.959	-0.097	0.513	-0.027	0.798	-0.069	0.605	-0.090	0.329
Wetland	0.054	0.703	-0.044	0.648	0.002	0.959	-0.029	0.758	0.053	0.632	0.054	0.703
Woodland/shrubland	0.083	0.670	0.003	0.951	-0.162	0.407	-0.238	0.167	-0.151	0.430	-0.217	0.248

2020

Land categories	Average wingspan		Voltinism		Hostplant specialization		Hostplant category		Overall specialization		Over-wintering stage	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Agriculture	0.013	0.923	-0.020	0.977	0.054	0.640	-0.005	0.933	-0.003	0.980	0.013	0.923
Barren	-0.051	0.695	0.104	0.416	-0.107	0.388	0.027	0.808	-0.099	0.489	-0.051	0.695
Disturbed	0.004	0.995	0.104	0.386	0.034	0.767	0.069	0.262	0.008	0.878	0.004	0.995
Forest	0.142	0.102	-0.030	0.772	0.074	0.517	0.054	0.580	0.148	0.148	0.142	0.102
Grasslands	-0.131	0.225	0.063	0.623	-0.116	0.314	-0.025	0.858	-0.155	0.165	-0.131	0.225
Shrublands	0.067	0.510	-0.076	0.490	0.088	0.436	-0.019	0.864	0.125	0.244	0.067	0.510
Unassigned	0.120	0.193	-0.060	0.612	0.049	0.752	0.017	0.869	0.151	0.172	0.120	0.193
Urban	0.049	0.645	0.010	0.934	0.150	0.092	0.024	0.801	0.105	0.448	0.049	0.645
Water	-0.081	0.335	0.036	0.779	-0.082	0.347	-0.028	0.742	-0.106	0.353	-0.081	0.335
Wetland	0.018	0.885	-0.019	0.932	0.056	0.588	-0.002	0.976	0.003	0.989	0.018	0.885
Woodland/shrubland	0.062	0.576	0.072	0.515	-0.096	0.425	0.099	0.427	-0.027	0.818	0.136	0.243

Table A.8. Flowering forb species richness, average number of flowering stems, and average total flowers per transect at six sites in north-central Oklahoma in June 2019 and 2020. Sites: BU= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Bison Unit, JD= John Dahl Wildlife Management Area (WMA), KAW= Kaw WMA, NT= The Nature Conservancy's Joseph H. William Tallgrass Prairie Preserve Nature Trail Area, RCU= Osage WMA Rock Creek Unit, and WWU= Osage WMA Western Wall Unit. Highest values bolded.

Site	Species Richness (S)		Flowering stems (Mean ± SE)		Total flowers (Mean ± SE)	
	2019	**2020**	**2019**	**2020**	**2019**	**2020**
BU	**19**	**11**	3.434 ± 0.43	**1.157 ± 0.26**	10.518 ± 1.90	9.173 ± 1.85
JD	4	2	2.071 ± 0.65	0.033 ± 0.03	3.571 ± 1.66	0.033 ± 0.03
KAW	11	10	**4.701 ± 0.56**	0.962 ± 1.28	9.506 ± 1.56	**12.508 ±2.24**
NT	10	8	3.053 ± 0.75	0.413 ± 0.15	**13.474 ± 7.55**	3.025 ± 1.15
RCU	8	**11**	2.735 ± 0.57	0.854 ± 0.18	7.324 ± 1.95	5.967 ± 1.56
WWU	9	8	1.773 ± 0.30	0.874 ± 0.15	3.864 ± 0.81	2.969 ± 0.76

Table A.9. The effect of flowering forbs on six butterfly community traits in north-central Oklahoma using a fourth-corner analysis. Values are presented as *r* (correlation coefficient), *p*.

Site	Species Richness (N)				Average flowering stems				Average total flowers			
	2019		2020		2019		2020		2019		2020	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Average wingspan	-0.046	0.614	0.009	0.466	-0.046	0.586	0.118	0.384	0.036	0.835	0.127	0.353
Voltinism	0.026	0.655	0.097	0.492	0.055	0.505	0.072	0.593	0.034	0.550	0.035	0.781
Hostplant specialization	-0.083	0.392	-0.011	0.393	-01.02	0.346	-0.141	0.288	-0.176	0.234	-0.110	0.393
Hostplant category	-0.022	0.814	0.097	0.734	-0.041	0.798	0.042	0.789	-0.197	0.122	0.069	0.597
Overall specialization	-0.072	0.397	-0.019	0.898	-0.083	0.395	-0.035	0.812	-0.157	0.296	-0.039	0.781
Over-wintering stage	-0.081	0.442	0.148	0.320	-0.016	0.913	0.099	0.522	-0.183	0.191	0.054	0.718

Figures

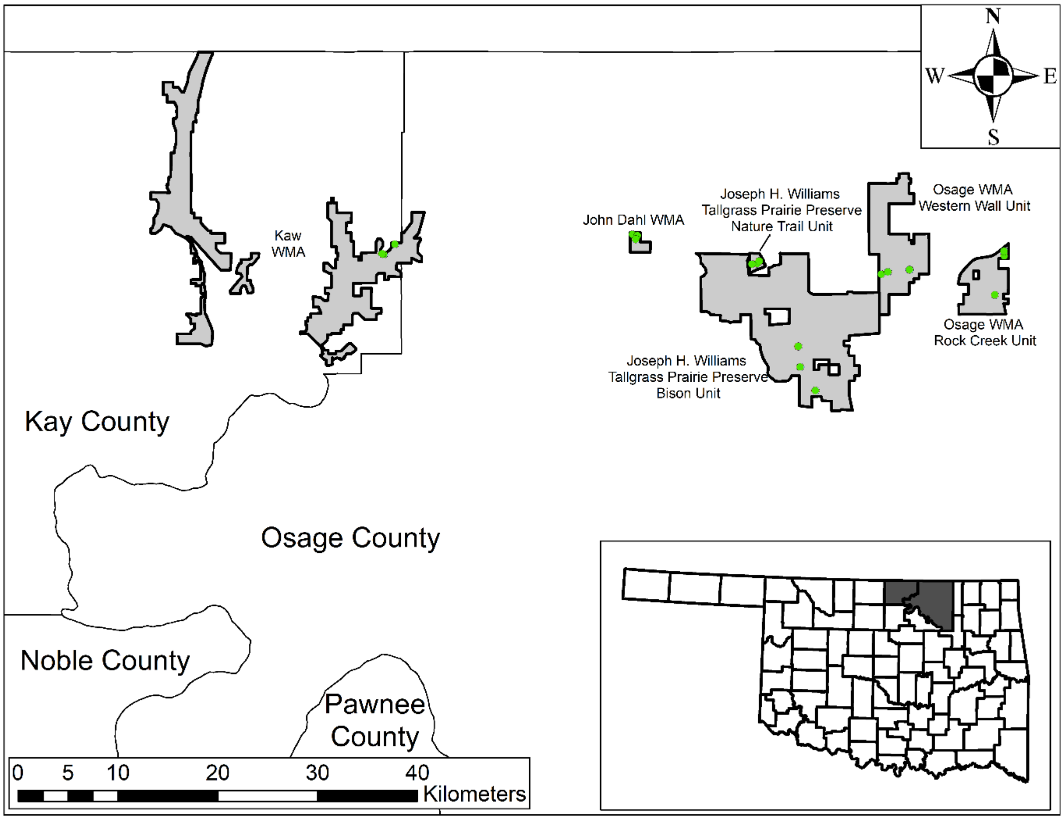

Fig. A.1. Map of study site locations in north-central Oklahoma. WMA = Wildlife Management Areas. Shaded areas are boundaries of sites and green points are transect starting locations. Insert depicts Oklahoma counties with Kay County and Osage County shaded. Study sites encompass a 34,186 ha area with 62.28 km the furthest separation between site transects (Kaw WMA and Osage WMA Rock Creek Unit) and 205.74 m separating the closest transects in Kaw WMA.

APPENDIX B

Chapter IV Supplementary Information

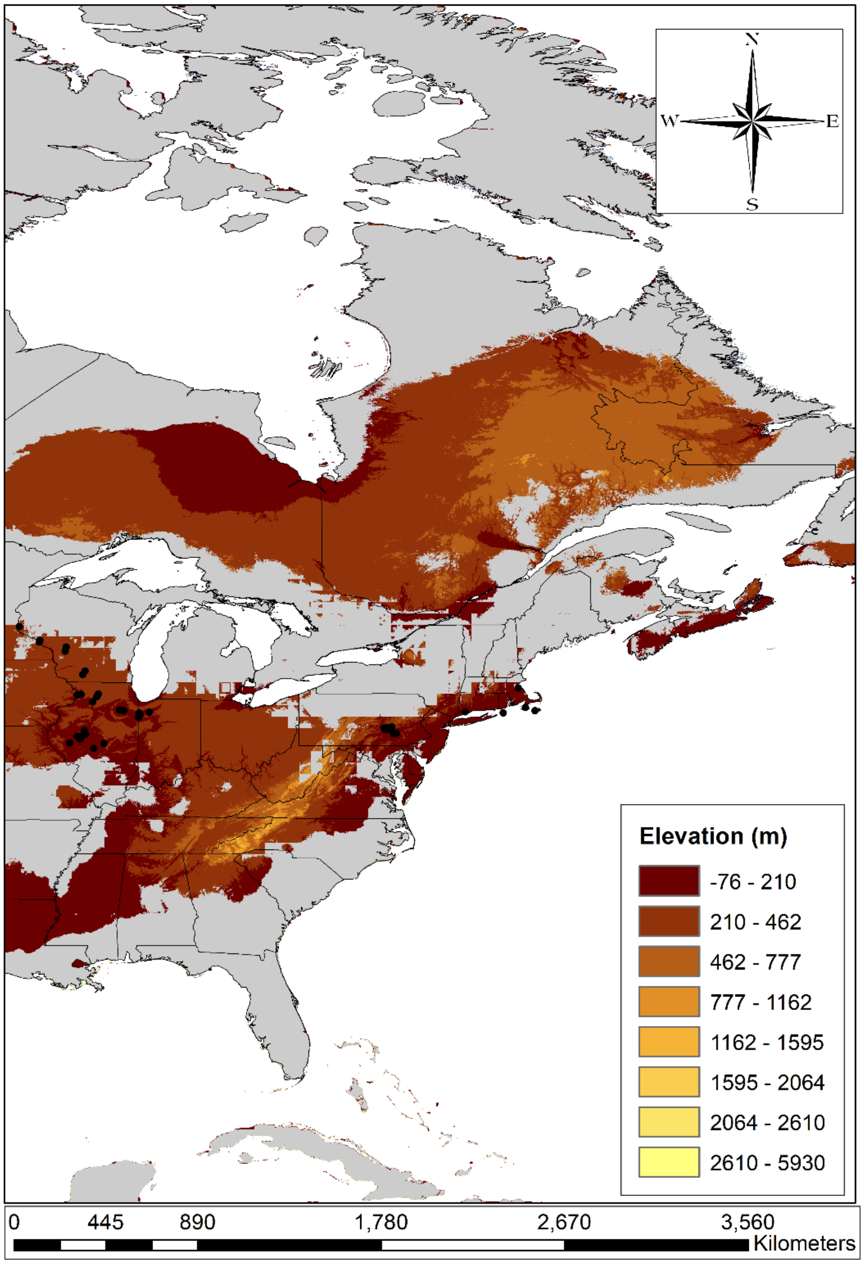

Fig. B.1. Elevation in regal fritillary (*Speyeria idalia*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

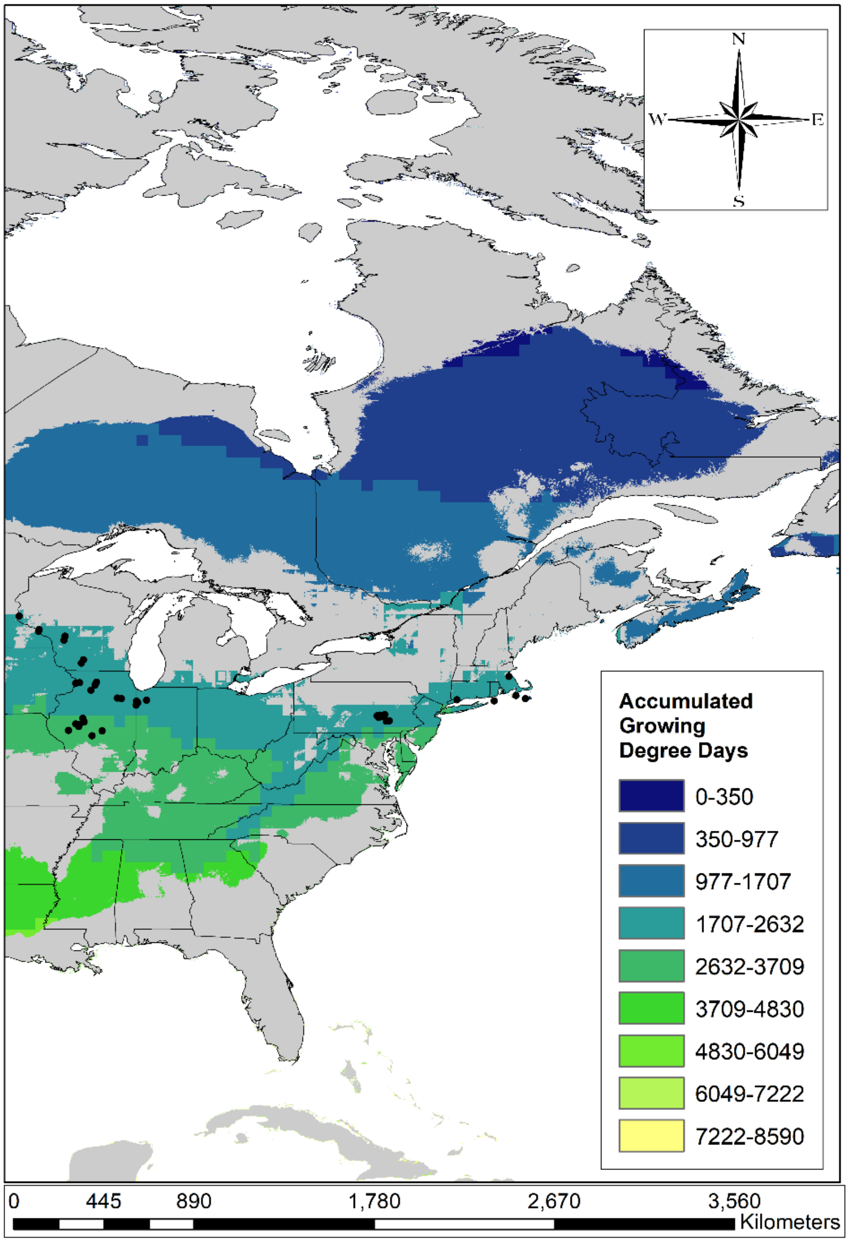

Fig. B.2. Accumulated growing degree days in regal fritillary (*Speyeria idalia*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

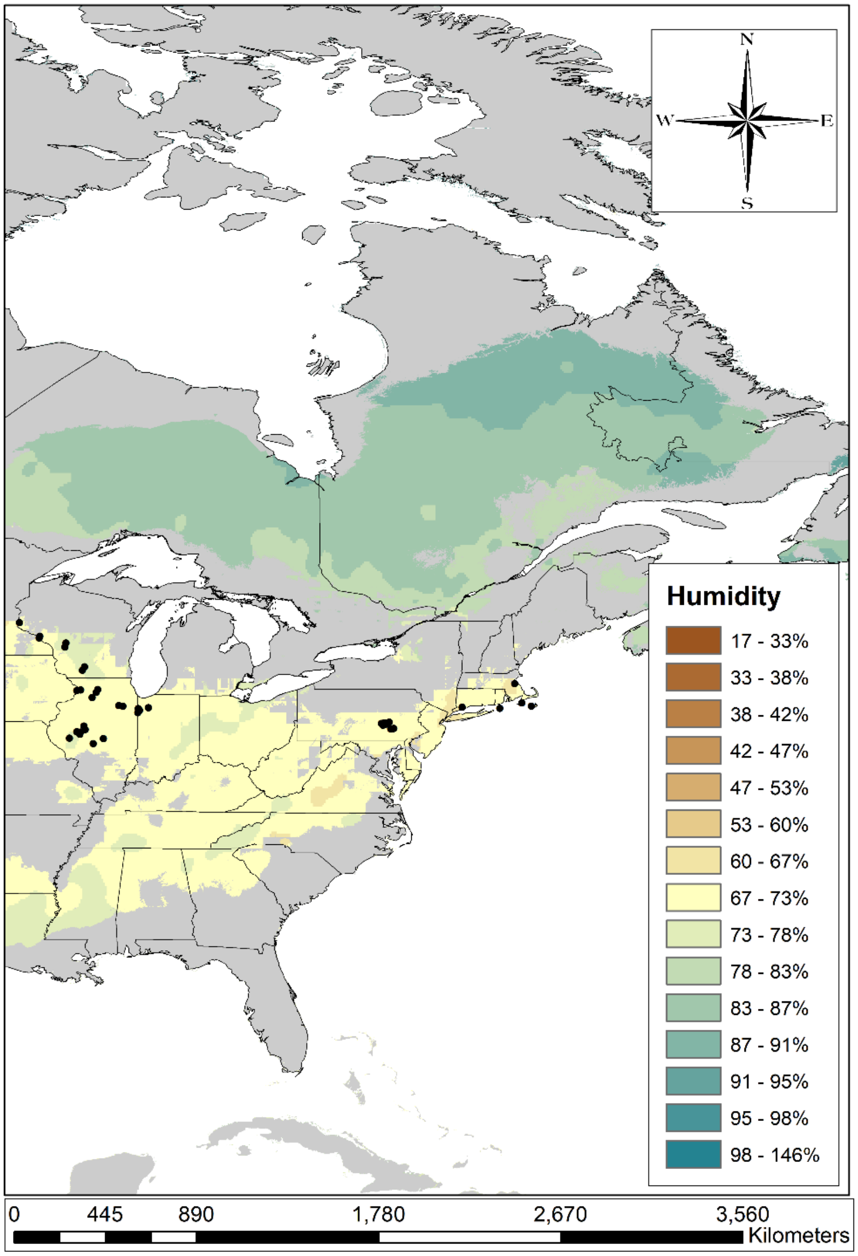

Fig. B.3. Average annual relative humidity in regal fritillary (*Speyeria idalia*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

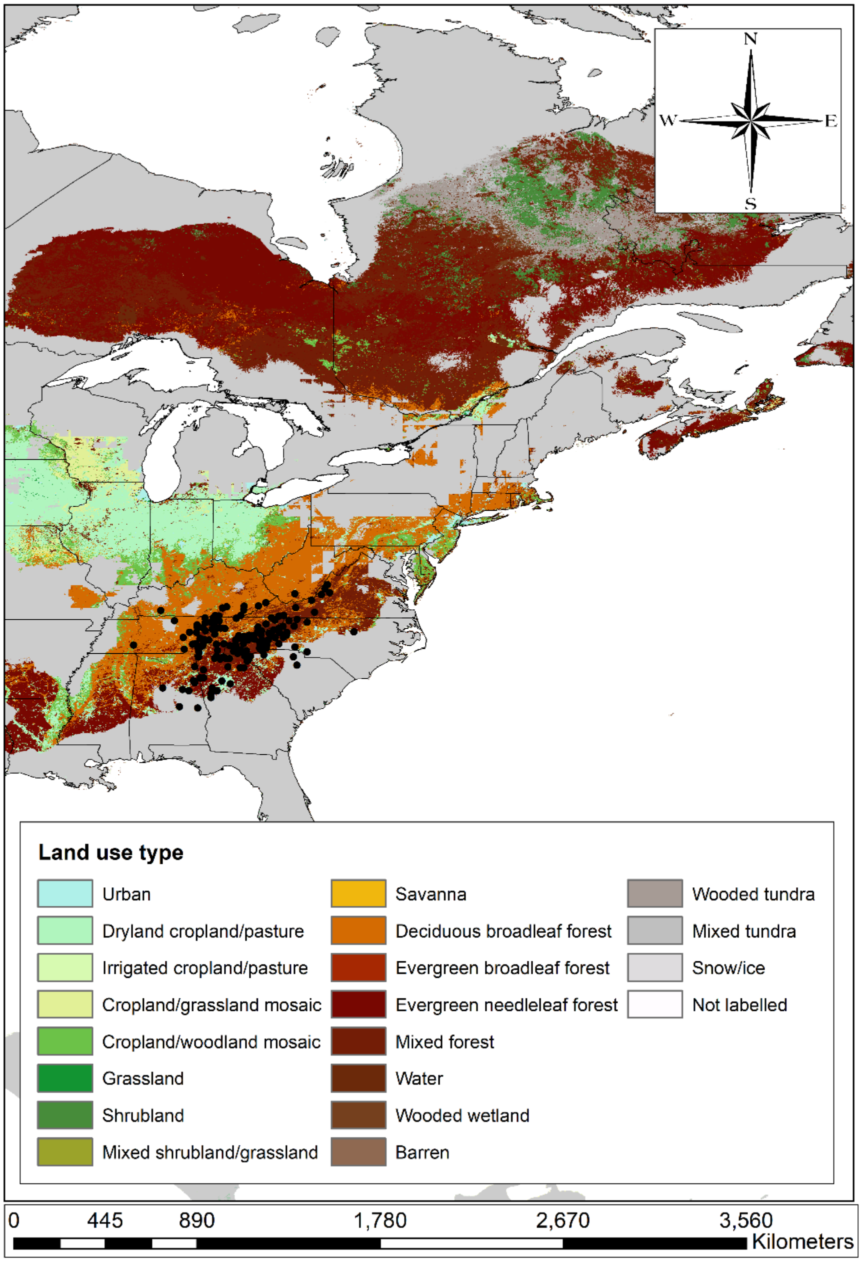

Fig. B.4 Land use types in Diana fritillary (*Speyeria diana*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

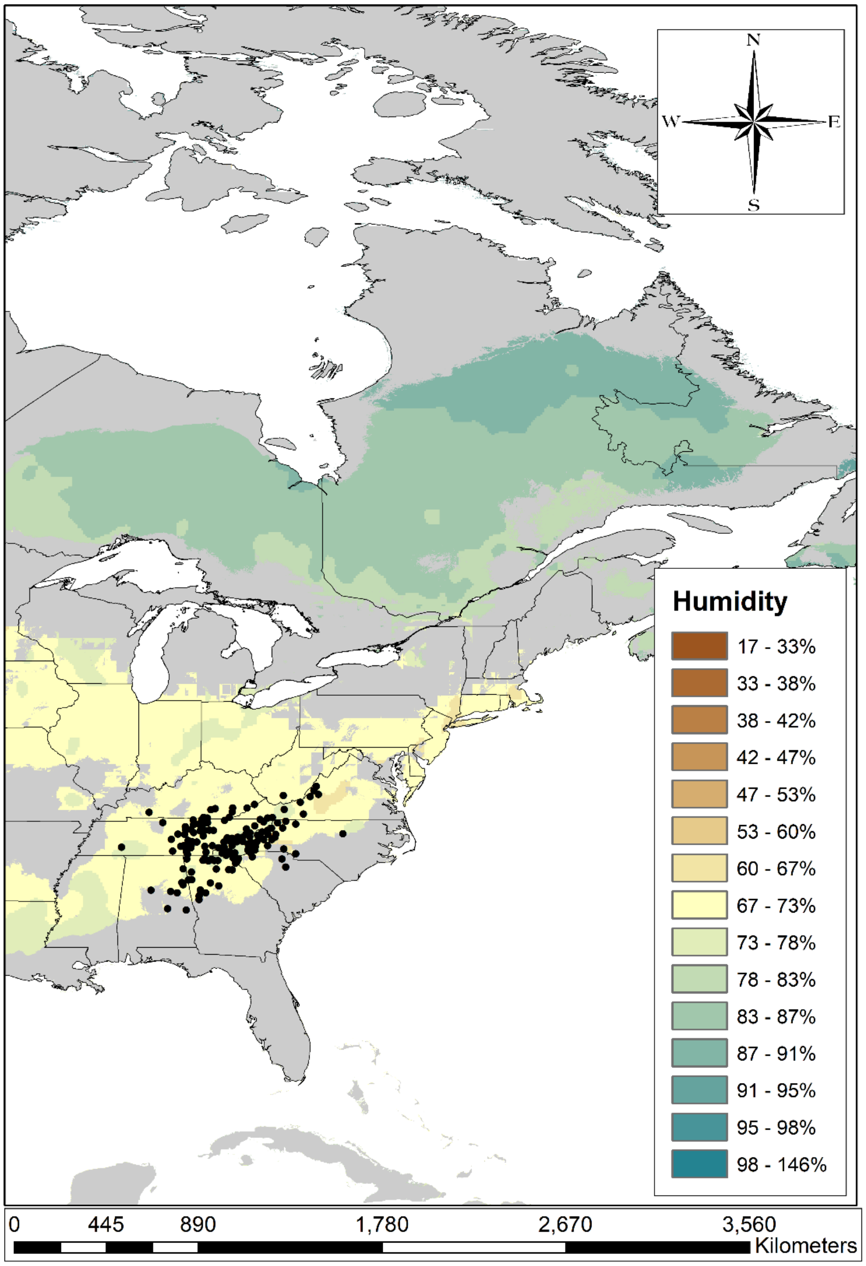

Fig. B.5. Average annual relative humidity in Diana fritillary (*Speyeria diana*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

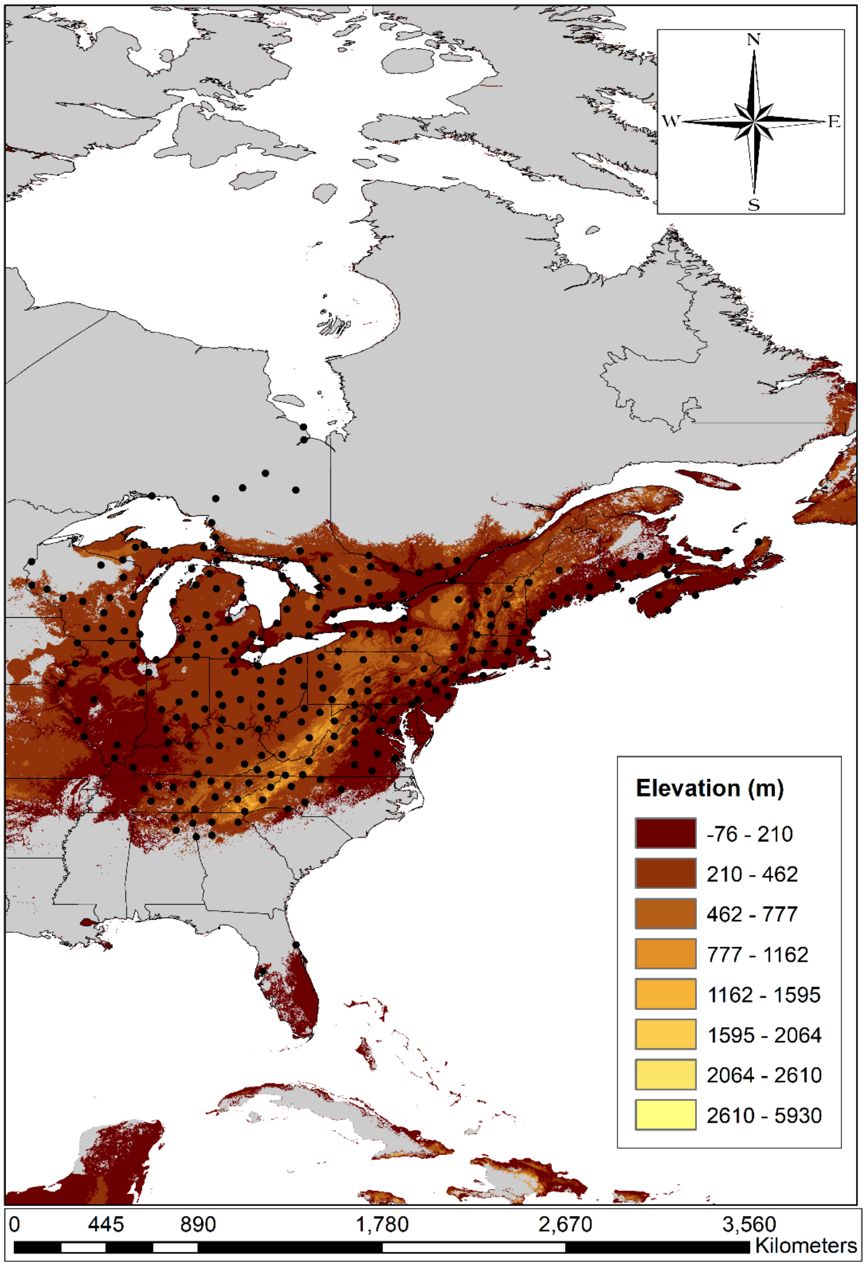

Fig. B.6. Elevation in great spangled fritillary (*Speyeria cybele*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

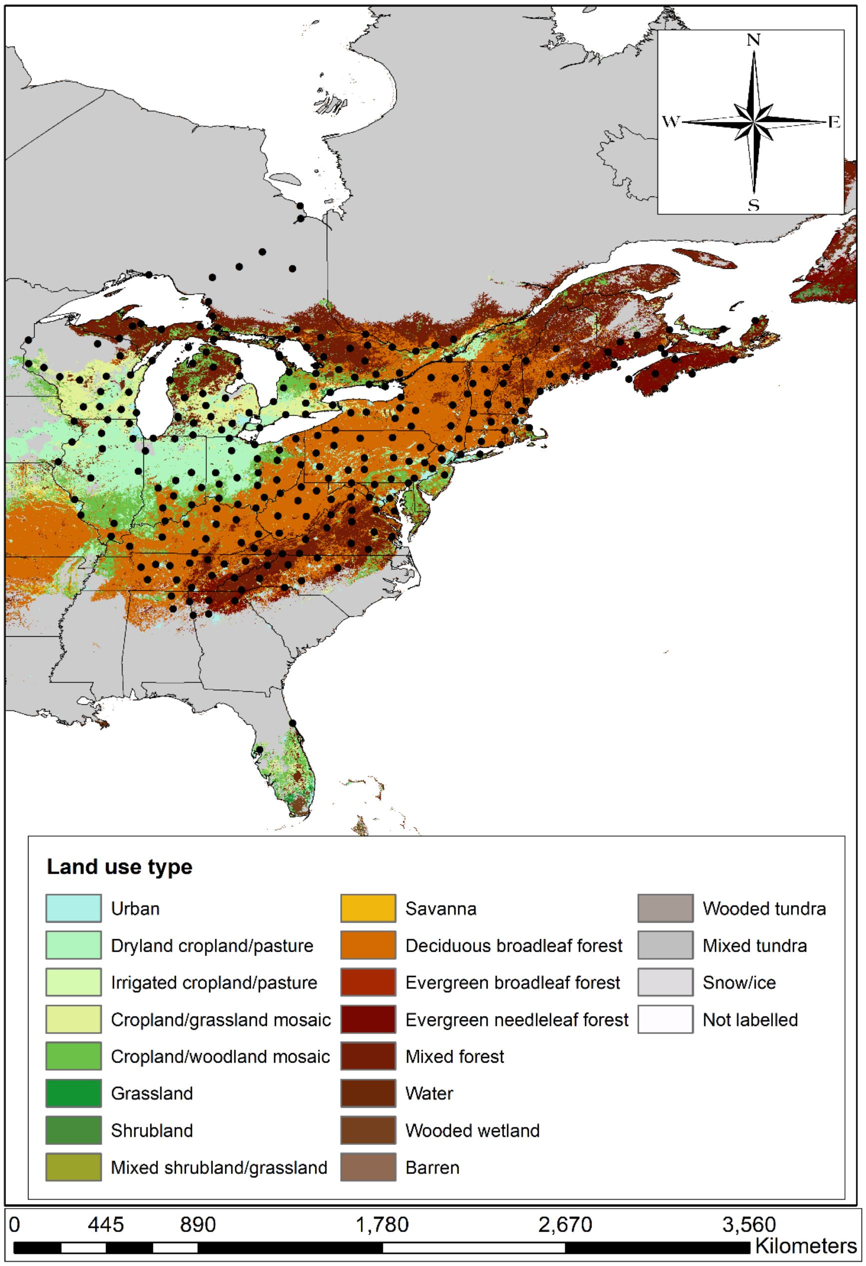

Fig. B.7. Land use types in great spangled fritillary (*Speyeria cybele*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

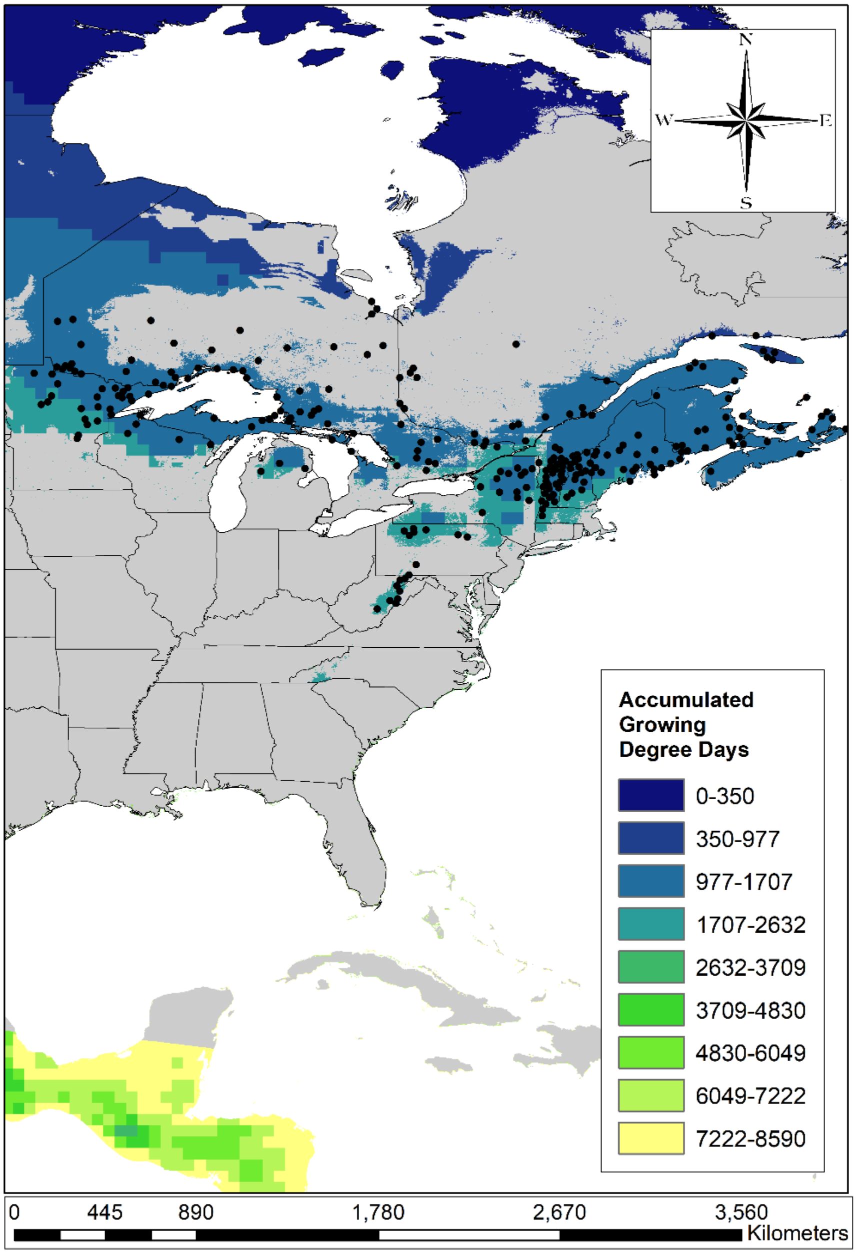

Fig. B.8. Accumulated growing degree days in Atlantis fritillary (*Speyeria atlantis*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

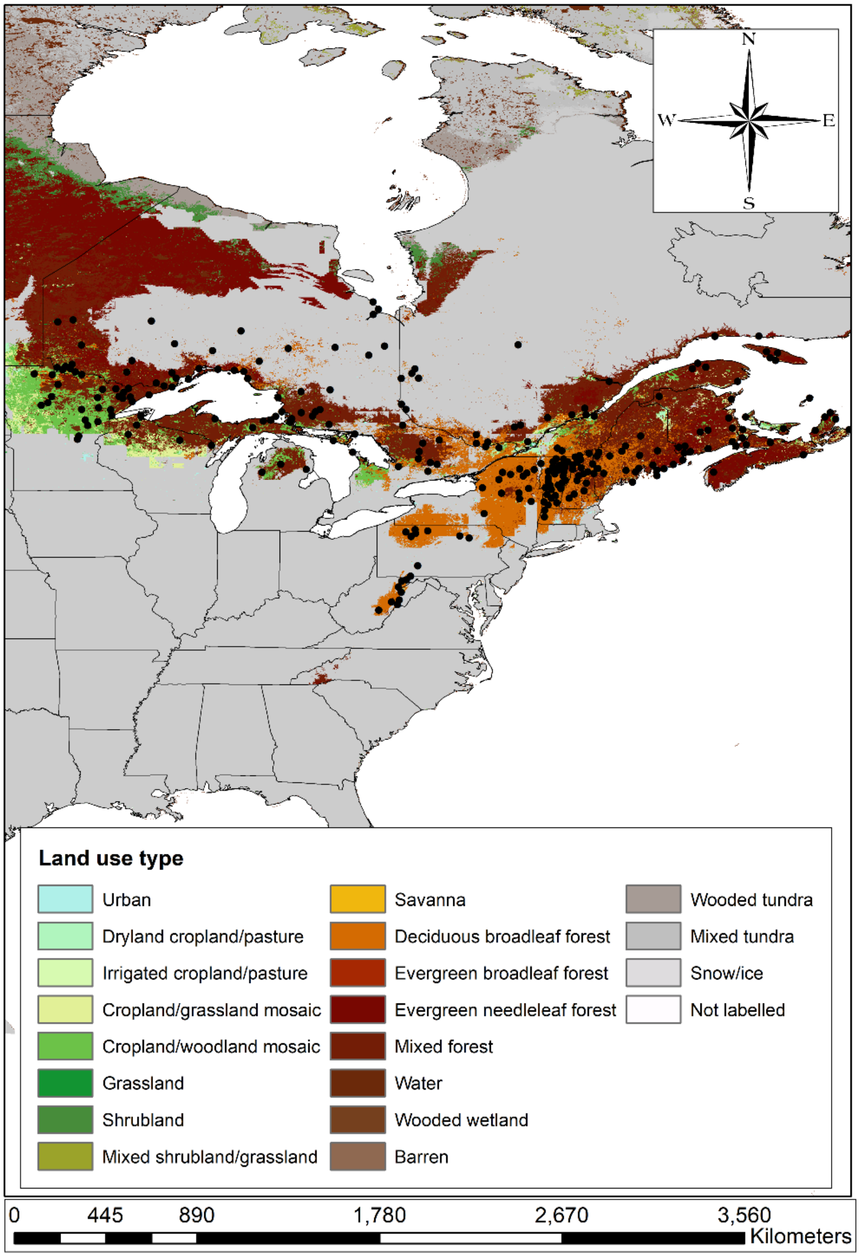

Fig. B.9. Land use types in Atlantis fritillary (*Speyeria atlantis*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

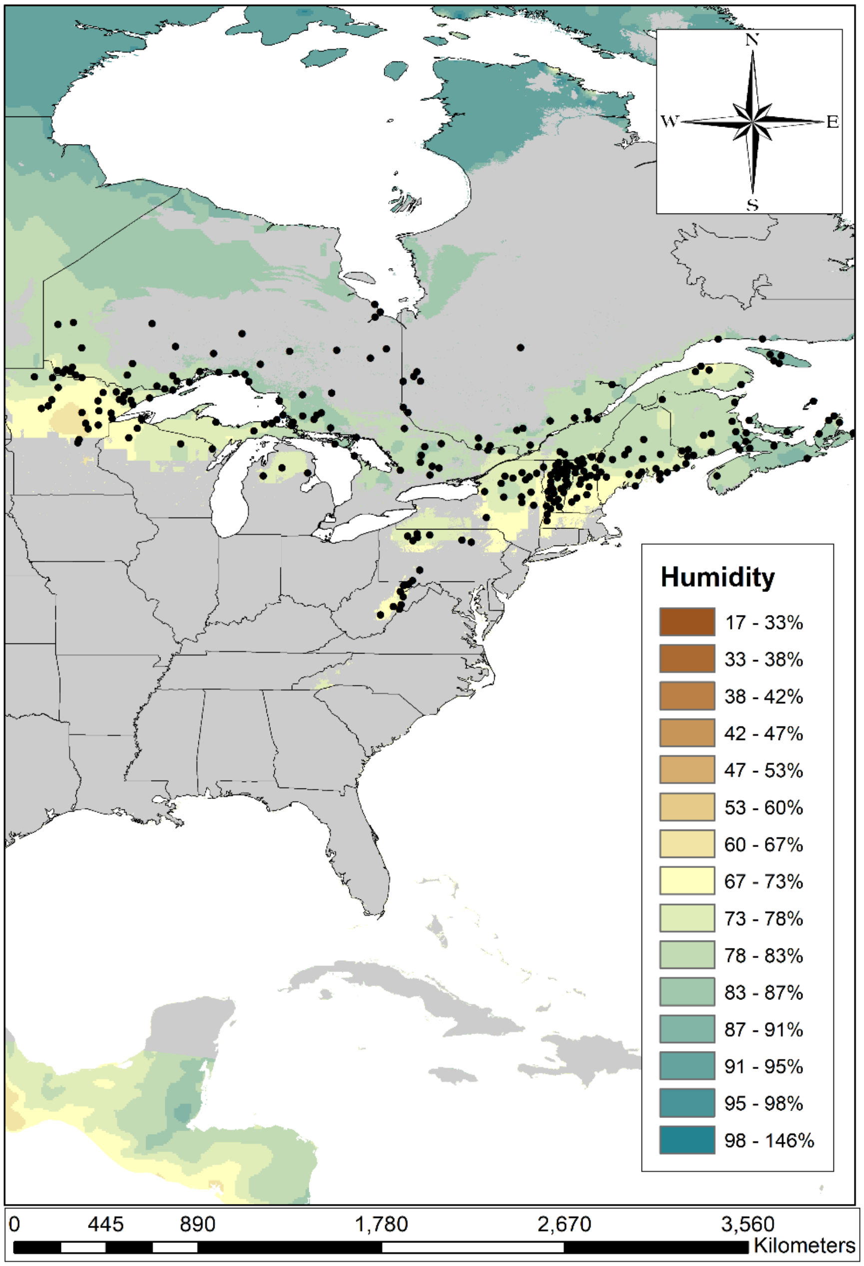

Fig. B. 10 Average annual relative humidity in Atlantis fritillary (*Speyeria atlantis*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

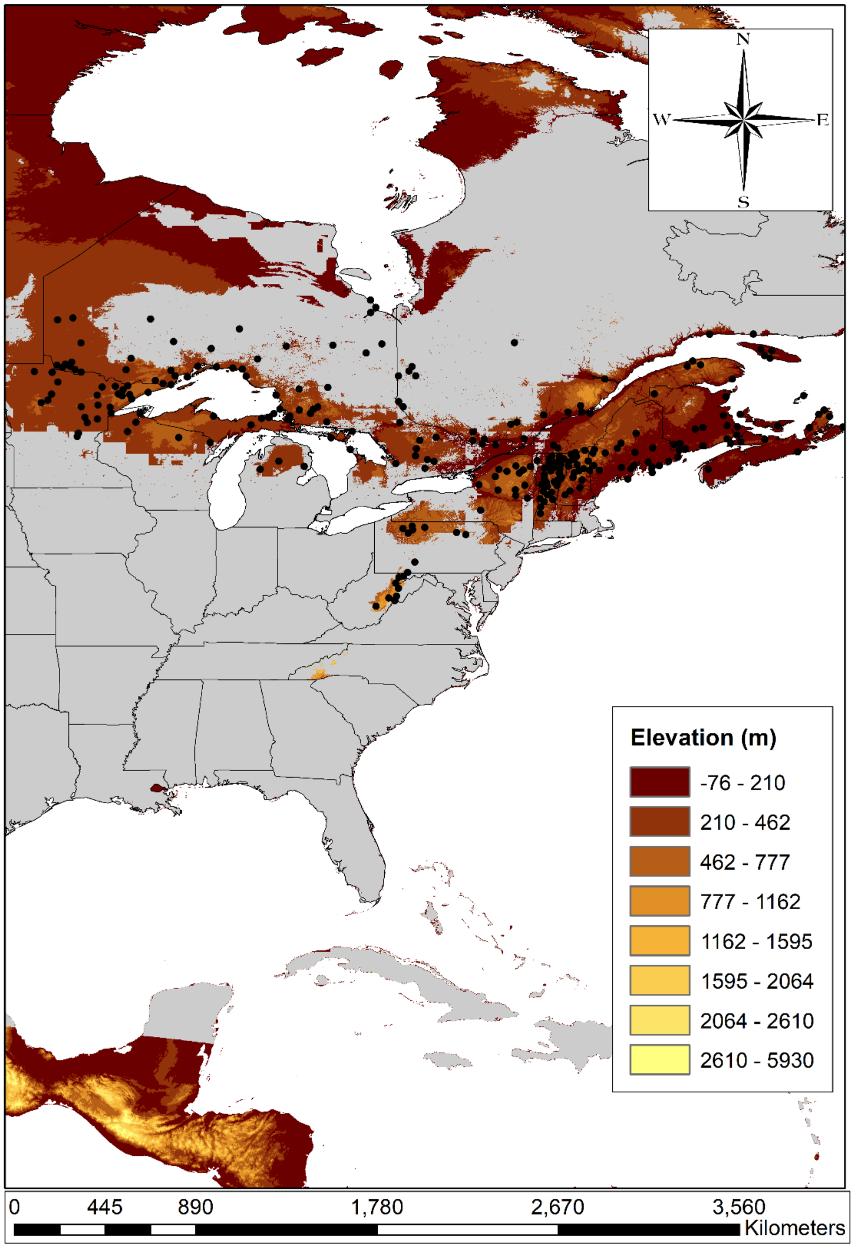

Fig. B.11. Elevation in Atlantis fritillary (*Speyeria atlantis*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

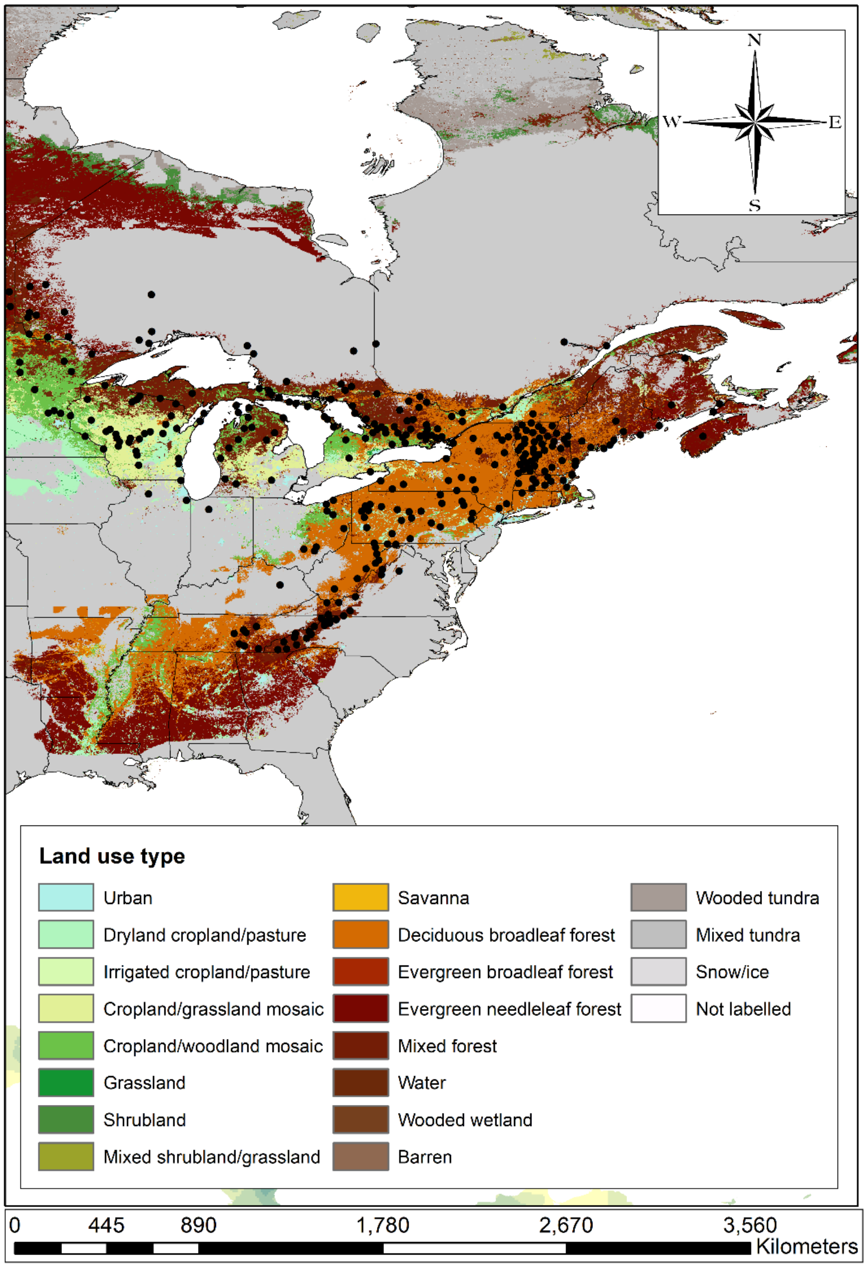

Fig. B.12. Land use types in Aphrodite fritillary (*Speyeria aphrodite*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

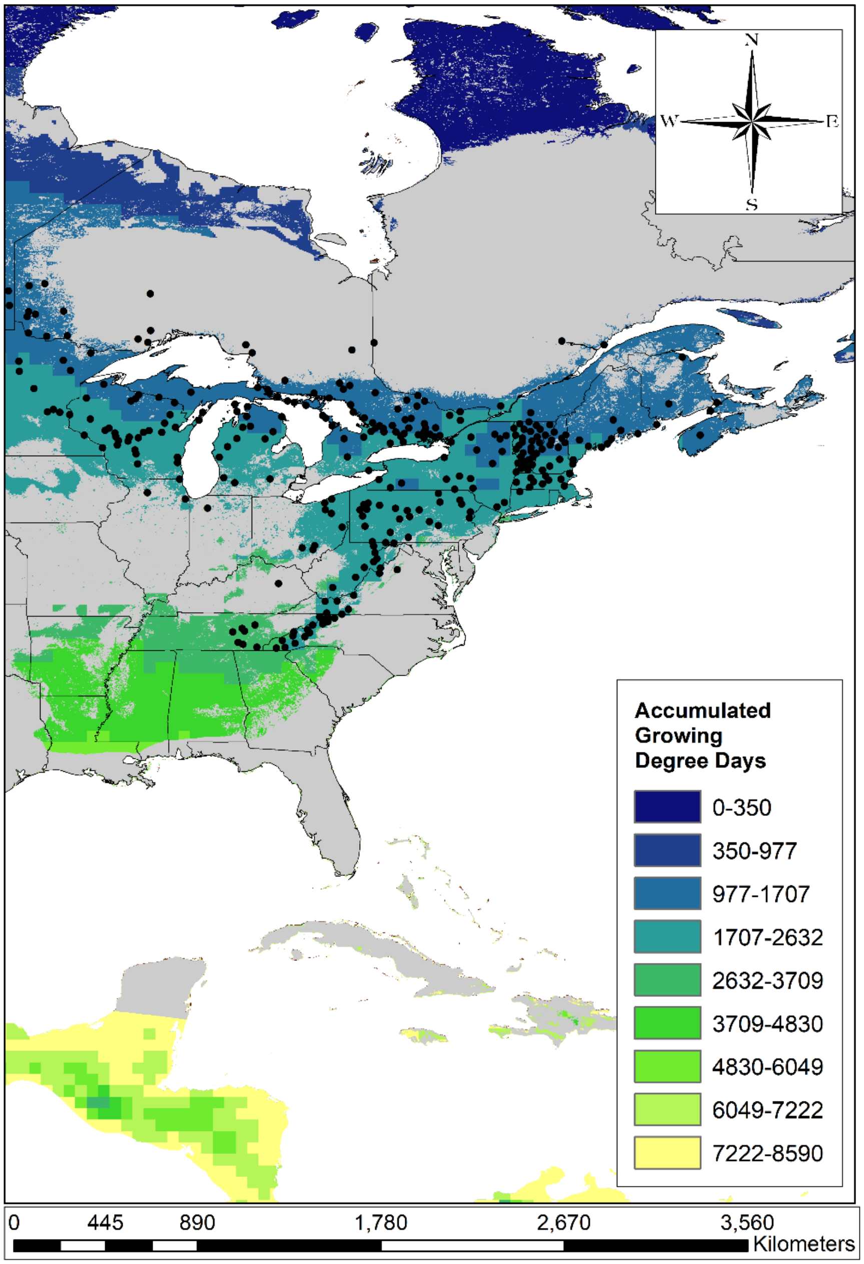

Fig. B.13 Accumulated growing degree days in Aphrodite fritillary (*Speyeria aphrodite*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

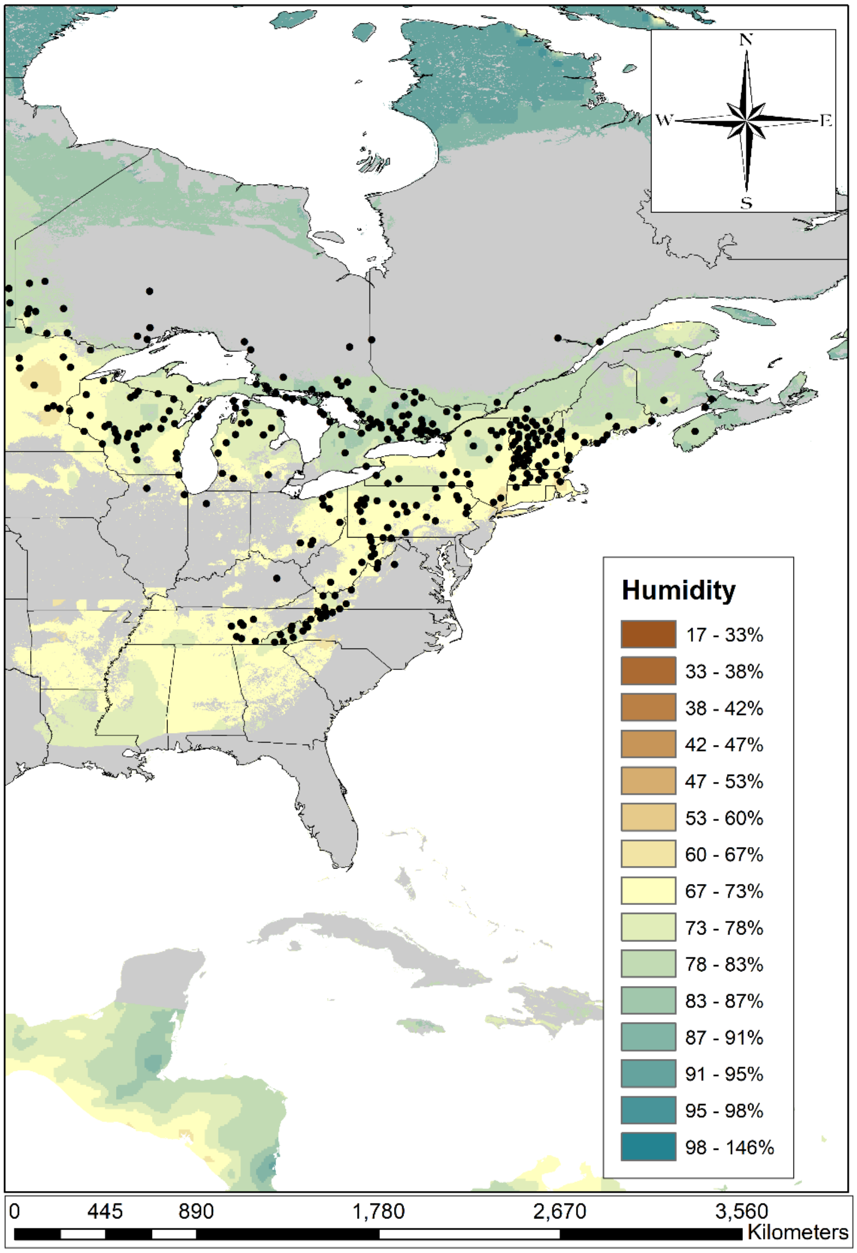

Fig. B.14 Average annual relative humidity in Aphrodite fritillary (*Speyeria aphrodite*) habitat with a probability occurrence of 30% or higher generated by an ecological niche model. Occurrence records are included as solid circles from January 1, 2000 to December 5, 2018.

VITA

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