GRASSLAND HETEROGENEITY AND PYRIC HERBIVORY: IMPLICATIONS FOR UNGULATE MOVEMENT, BIODIVERSITY CONSERVATION, AND RANGELAND PRODUCTIVITY IN THE ANTHROPOCENE

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Abstract: How to simultaneously manage grasslands for sustained livestock productivity and biodiversity conservation is a persistent dilemma for rangeland ecologists and conservationists. Moreover, climate change and invasive species are recognized as potential threats to many grassland management and conservation objectives. Pyric herbivory – the recoupling of fire and grazing – promotes grassland heterogeneity that is critical to meeting biodiversity, livestock, and invasive species objectives. While fire and physical landscape characteristics (i.e., slope, elevation, aspect, etc.) significantly affect ungulate behavior, it remains unknown how their movement changes with the ambient landscape (i.e., weather, diurnal cycles, seasonal rhythms). The feedbacks between ungulate movement and landscape characteristics – particularly those driven by fire – can also have significant effects on plant communities. However, how feedbacks between invasive species, fire timing, and management (e.g., herbicide, or the interactive effects of fire and herbicide) affect plant dynamics and livestock production remains unknown. Extant knowledge is restricted to studies at small scales unrepresentative of large complex grasslands. Therefore we conducted four distinct studies across grasslands managed with pyric herbivory: two addressing how seasonal, diurnal, and meteorological patterns (e.g., temperature) affect bison movement patterns; and two investigating how invasive species and management approaches aimed at their reduction affect livestock productivity and grassland plant assemblages at multiple scales ($0.1\text{m}^2 – >10^6\ \text{m}^2$). We found that bison movements change with season and time of day, and are most affected by air temperature compared to other weather parameters. We also determined that invasive species management may not increase livestock production or biodiversity across large grasslands (i.e., >300 ha), and relationships between invasive species abundance and plant diversity changed with scale. Scale is regarded as a central problem in ecology, and therefore managers should be cautious when applying results from small scale studies to large landscapes. Moreover, landscape heterogeneity is well documented as fostering biodiversity maintenance and ecological resiliency. Therefore, heterogeneity – and processes that promote it – will be critical to conserving grassland biodiversity and function throughout the Anthropocene.

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CHAPTER I

ARE BISON MOVEMENTS DEPENDENT ON SEASON AND TIME OF DAY? INVESTIGATING MOVEMENT ACROSS TWO COMPLEX GRASSLANDS

Abstract

The American plains bison (*Bison bison*) is an iconic herbivore on North American grasslands, yet many questions surrounding their basic biology remain unanswered. We analyzed fine-resolution movement data (12 minutes) from two of the largest remaining prairie tracts in the Great Plains of North America to address whether bison movement and distance travelled are affected by seasonal or diurnal rhythms. We fit binomial movement and movement distance data to generalized linear mixed models to test whether site, season, or time of day affected movement. Our top models included season-site and season-time of day interactions as fixed-effects. Overall, bison were more likely to move during the day than at night regardless of season or site. There was considerable overlap between our sites across most seasons, with the strongest divergence occurring in autumn for movement probability and distance. During the summer, daytime bison movement declined in favor of nighttime movement, potentially in response to high temperatures. Day and nighttime movement distance and probability both were lowest in the winter. That site alone was not a significant predictor of bison movement or movement distance may suggest that their response to seasonal and diurnal rhythms is biologically innate.

Therefore, we conclude that season and time of day should be considered in future bison movement analyses. Here we present the first replicated analysis of fine-resolution, seasonal and diurnal bison movements across two large complex landscapes using a long-term dataset. As ungulate behavior changes in response to the Anthropocene, filling the knowledge gaps in their basic biology is critical to their continued conservation.

Key words: American plains bison, ecology, prairie, conservation, landscape, ungulate movement, seasonality, diurnal rhythms

Introduction

Since their decline in the 19th century, American bison (*Bison bison* L.) have become an icon for many grassland restoration and conservation organizations in North America. Many of these groups cite hypothesized keystone effects that bison may have on grassland ecosystems as a rationale for some of the reintroduction projects that are ongoing (Fuhlendorf et al., 2018; McMillan et al., 2019). However, there is evidence that these effects are often confounded with management actions, and may not be due to bison reintroduction alone (Allred et al., 2011b; Fuhlendorf et al., 2018). Rather, research suggests that the interaction between bison (and other grazers) and disturbance-processes (e.g., fire) may have a more significant influence on grassland ecosystems than grazer species alone (Allred et al., 2011b). The feedback between grazing behaviors and fire disturbance, in particular, increases landscape complexity, which is critical to maintaining grassland biodiversity (Fuhlendorf et al., 2009a). While we know a great deal about where bison move, we know very little about the mechanisms influencing their movement decisions.

Animal movement and behavioral studies, including those of bison, have historically been limited to visual or high frequency radio-tracking studies because of the high-costs, or practical difficulties associated with using fine-resolution (< 3m accuracy), high fix-rate (< 1 hour per fix) global-positioning system (GPS) tracking technology (Tomkiewicz et al., 2010). These limitations have kept nighttime movements and fine-resolution behavioral patterns unknown for many species, including some charismatic megafauna (Owen-Smith and Goodall, 2014; Tomkiewicz et al., 2010). Recently, however, researchers have shown that some ungulates alter their non-migratory movement patterns in response to seasonal (Owen-Smith and Goodall, 2014; Schmidt et al., 2016) and diurnal (Hazlerigg and Tyler, 2019) rhythms. Unlike many ungulates that track seasonal shifts in forage quality (Merkle et al., 2016), there is currently no conclusive evidence suggesting that bison movement shifts seasonally (Geremia et al., 2019). To date much of our bison ecology knowledge is based on studies of small, homogenously managed landscapes, and single or small herds (Allred et al., 2011b; Fuhlendorf et al., 2010; Towne et al., 2005). Historically, bison would have roamed large, complex, and unfragmented landscapes (Fuhlendorf et al., 2009a; Hornaday, 1889). Therefore while previous studies have provided valuable insights into bison behavior, they may not reflect behavioral responses to complex landscapes critical to grassland biodiversity (Fuhlendorf et al., 2009a). Additionally, almost all of what we know about bison behavior on complex landscapes is skewed toward habitat or resource selection models (i.e., point pattern analyses; Edelhoff et al., 2016) based primarily on the spatial distribution of somewhat temporally-fixed landscape features such as topography or the distribution of water bodies (e.g. Allred et al., 2011; Kohl et al., 2013). Thus, there is a distinct knowledge gap surrounding how bison move in general, let alone how they move with seasonal and diurnal rhythms.

We had the opportunity to use a robust bison movement dataset from two well-known herds in the Southern Great Plains to address these fundamental gaps in our knowledge about bison movement. Seasonal and diurnal rhythms are known to affect ungulate movement broadly (Johnson et al., 2002; Owen-Smith et al., 2012; Owen-Smith and Goodall, 2014), but the importance of these basic and critical factors has been mostly overlooked for American bison. Therefore, as many bison reintroduction projects are ongoing across the Great Plains (Fuhlendorf et al., 2018; McMillan et al., 2019), addressing gaps in our fundamental understanding of bison movement has significant management and conservation value. We conducted this descriptive study asking: (1) does bison movement probability, and (2) distance change between seasons and times of day; or are they better explained by differences between the two independent herds and landscapes alone? Overall, we hoped to determine whether movement patterns across seasons and times of day were consistent across two independent sites.

Methods

Study areas

The data we used in our study were collected across two sites in Oklahoma that vary considerably in their management, topography, vegetation, and climate: The Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve (TPP) and the United States Fish and Wildlife Service's Wichita Mountains Wildlife Refuge (WMWR). The TPP, located in Osage County, Oklahoma is an approximately 16,000-ha tract located at the southern end of the Flint Hills ecoregion of North America. The TPP is dominated by vegetation typical of a productive tallgrass prairie ecosystem (e.g., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Dalea candida* Michx. Ex Willd., *Echinacea pallida* (Nutt.) Nutt., *Liatris* spp., *Asclepias* spp., etc.; Table 1.1). Temperature and precipitation are highly variable across the TPP, which is typical for grassland ecosystems globally, but averages range from 13 to 16 °C and 100 to 200 cm annually (Brock et al., 1994; McPherson et al., 2007; Table 1.1). The TPP is divided into two distinct units based on the dominant grazer (cattle or bison), and our study focused on data collected in the 9,400-ha bison unit (~72% of the total preserve area) where approximately 2,500 bison are allowed to freely graze year-long. Most of the TPP is managed with fire under the patch-burning management paradigm that is focused on restoring structural heterogeneity on the landscape (Hamilton, 2007). Fire in the TPP bison unit is randomly applied across the unit, with time-since-fire ranging from 0-6 years across all of the patches. Bison at the TPP focally graze recently burned patches disproportionately more than those that were burned previous years, creating a temporally and spatially shifting mosaic of grassland structure across the area (Allred et al., 2011b; Hamilton, 2007). Fire is applied at various times throughout the year in the TPP bison unit to mimic historic fire regimes (Hamilton, 2007).

The WMWR is a 23,884-ha refuge managed by the U.S. Fish and Wildlife Service in Comanche county, Oklahoma. The WMWR is made up of several ecosystems that vary with elevation (range: 422-755 m above sea level; Table 1.1), but the grasslands occurring throughout the refuge are characterized as mixed-grass prairie (e.g., *Schizachrium scoparium* (Michx.) Nash, *Bouteloua gracilis* (Kunth) Lag. ex Griffiths, *Comandra pallida* (A. DC.) Piehl, *Penstemon albidus* Nutt., *Agrostis elliottiana* Schult., *Aristida purpurea* Nutt., etc.; Table 1). Precipitation and temperatures are variable at the refuge. Precipitation is much lower on average (27 to 66 cm; Table 1.1) than at the TPP, but temperatures were similar to TPP (10 to 16 ℃; Brock et al., 1994; McPherson et al., 2007; Table 1.1). WMWR is actively managed with prescribed fire and grazing, although unlike the TPP, the approximately 650 bison and 220 longhorn cattle at the WMWR are free to graze jointly across the majority of the refuge.

Data collection

For this study, we utilized GPS-telemetry data from the TPP and WMWR bison herds, collected across multiple temporal resolutions (Allred et al., 2011a). GPS-collars were deployed on seven female individuals from the TPP, and six female individuals from WMWR from November

2008 – November 2010 and November 2010 – July 2012, respectively. Collar location data were recorded at 12 minute temporal intervals for all individuals. When recorded across long-temporal intervals, ungulate movement data (particularly those of bison) may be confounded by fence-effects, or other restrictions to movement correlated to restrictive, manmade landscape features. Therefore, our use of 12-minute data collection allowed us to reduce the effect of fences and other barriers on our movement analyses. From 2008 – 2010, patches within the TPP bison unit were annually burned and the unit was moderately stocked (2.1 AUM · ha^{-1}; One animal unit month [AUM] is equal to the forage required to feed one 454 kg cow and calf for one month) across a 9,400-ha unit. From 2010 to 2012, the WMWR did not have a fixed burn schedule and was lightly stocked with bison (0.32 AUM · ha^{-1}) and longhorn cattle (0.11 AUM · ha^{-1}). The location data we acquired were differentially corrected using GPS base stations located on TPP and WMWR (Allred et al., 2011a).

Data analysis

To investigate how diurnal, seasonal, and site affect bison movement patterns we calculated movement metrics from our GPS data and stratified them by season and time of day. We used the package “amt” in R (R Core Team, 2021; Signer et al., 2019) to clean and process all of our GPS-data prior to analysis. We resampled the entire dataset using our fix-rate to ensure that each movement track represented an uninterrupted series of 12-minute movements for each individual in our dataset (Barnett and Moorcroft, 2008; Signer et al., 2017). Next we calculated the distance travelled for each 12-minute movement in our grouped and processed dataset using the function step_length (Signer et al., 2019). Using movement distance, as opposed to other primary movement measures, allowed us to most simply and effectively detect state-changes typical in non-migratory ungulates through time (Edelhoff et al., 2016). We used the function time_of_day (Signer et al., 2019) to determine whether a movement occurred during the day or night (factor with two levels), which were determined following official sunrise and sunset times for the specific date that a movement occurred. We also assigned a season (i.e., spring, summer, autumn, or winter; a factor with four levels) to each movement based on its calendar date using the time-stamp for each GPS-fix.

We use generalized linear mixed models with binomial link functions to form alternative models of the probability of movement being affected by site, season, and/or time of day. We quantified the support the data provided for those models using Akaike Information criterion. We classified all movements less than 3-meters as non-movements (recorded as 0), as this distance was within the error rate for the collars, and all movements greater than 3-meters as a movement (recorded as 1). We then used the R package lme4 (Bates et al., 2015) to develop multiple generalized linear mixed models using all pairwise combinations of site, season, and time of day as fixed effects with individual used as the random intercept.

We used gamma distributed generalized linear mixed models with log link functions to investigate whether bison movement distances were affected by site, season, and/or time of day. We quantified the support the data provided for those models using Akaike Information criterion. We included individual i.d. number as the as the random intercept parameter for each model. We developed mixed-effects models for all pairwise combinations of site, season, and time of day as fixed effects.

Results

We analyzed 554,971 total data points in this study, with nearly 70% of those coming from the TPP (n = 391,195) and the remaining 30% from the WMWR (n = 163,776). The mean 12-minute step length across all of our sites was 55.3 m, with a standard deviation of 107 m (se = 0.1 m), and mean step lengths at TPP and WMWR were 57.5 m (SD = 112.5 m) and 49.8 m (SD = 92.4 m), respectively.

Movement probability

Season-site and season-time of day pairwise interactions best described the probability of bison movement compared to our other models (Table 1.2). Although observed relative movement frequencies between our sites were not clear across all seasons, the most divergence occurred in the autumn (TPP: x̄ = 0.79, SD = 0.02; WMWR: x̄ = 0.74, SD = 0.04; Figure 1.1). Overall, we found that bison were more likely to move during the day than at night across all seasons (Figure 1.2). Following predictions from our top model, our observed bison movement frequencies changed seasonally where bison moved most often during the day in the winter than any other time and season (x̄ = 0.89, SD = 0.02; Figure 1.2). Our observed nighttime relative movement frequencies rose to their peak from spring (x̄ = 0.68, SD = 0.03) to summer (x̄ = 0.72, SD = 0.06), and were lowest in the winter (x̄ = 0.65, SD = 0.05; Figure 1.2). Conversely, our observed daytime relative movement frequencies declined to their lowest from spring (x̄ = 0.87, SD = 0.01) to summer (x̄ = 0.83, SD = 0.03), and then steadily rose to their peak from autumn (x̄ = 0.87, SD = 0.02) to winter (x̄ = 0.89, SD = 0.02; Figure 1.2).

Movement distance

The distance that bison move during a single movement event is best described by season-site and season-time of day pairwise interactions compared to all of our other models (Table 1.2). For most of the year bison movements were similar between our two sites (Figure 1.3). However, the clearest difference between the two sites occurred in Autumn (TPP: x̄ = 61.1 m, SD = 103.7; WMWMR: x̄ = 43.6 m, SD = 81.4; Figure 1.3). The mean distance travelled for a single movement event for our bison was always higher during the day than at night regardless of season (Figure 1.4; Table 1.3). Our observed mean distance travelled during the day was relatively constant during the spring (x̄ = 73.2 m, SD = 114.3, n = 95,710), summer (x̄ = 77.2 m, SD = 140.2, n = 89,016), and autumn (x̄ = 76.7 m, SD = 109.7, n = 39,434); but was lowest in the winter (x̄ = 55.5 m, SD = 103.3, n = 61,075; Figure 1.4). Mean nighttime distances peaked from spring ($\bar{x}$ = 42.0 m, SD = 96.6, n = 80,106) to summer ($\bar{x}$ = 57.9 m, SD = 109.5, n = 62,412), but then declined from autumn ($\bar{x}$ = 37.5 m, SD = 82.0, n = 43,470) to winter ($\bar{x}$ = 21.0 m, SD = 51.3, n = 83,748; Figure 1.4).

Discussion

Much of the literature on bison ecology is focused on analyzing single herds that roam small, homogenously managed landscapes (Allred et al., 2011b; Fuhlendorf et al., 2010; Towne et al., 2005). To the best of our knowledge, our study represents the first analysis of seasonal and diurnal bison movements using data from two distinct herds on large complex landscapes. Further, even though our sites differed in size, topography, management, vegetation, forage productivity, and precipitation (Table 1.1) we found that bison movement probability and distance may be more affected by seasonal and diurnal rhythms than site differences alone. This is especially notable since one of our sites – the Tallgrass Prairie Preserve – is managed primarily to maximize structural heterogeneity (Hamilton, 2007). The variability in movement distance between our two sites (Table 1.3) is likely due to the topographical differences between the two sites as bison generally avoid steep slopes (Table 1.1; Allred et al., 2011a; Kohl et al., 2013), restricting movement at the WMWR more than at the TPP. That movement distances were more variable at the TPP than at the WMWR may also be due in-part to the shifting spatial arrangement of fire at the TPP (i.e., patch-burning; Hamilton, 2007), which significantly alters bison resource selection (Allred et al., 2011a). Our results follow recent studies elsewhere showing that seasonal and diurnal rhythms generally have strong effects on ungulate movement decisions (Owen-Smith and Goodall, 2014). Therefore, we conclude that season and time of day should be considered as important predictors of bison movement in future studies.

We found that bison movement and distance travelled were partially explained by the interaction between season and time of day, which drive many landscape and life history patterns that are known to affect movement. For example, seasonal and diurnal rhythms both work to drive many landscape patterns like vegetation distribution and quality (Geremia et al., 2019). As ungulates, bison movement decisions are significantly affected by forage quantity, quality, and distribution across landscapes (Fortin et al., 2003; Geremia et al., 2019), all of which are partly driven by seasonal and diurnal rhythms in photosynthesis (Pilarski, 1999) and weather. For example, that our observed bison movement distances were more variable overall during the day than at night may be partly explained by differences in forage quality, as ungulate movement rates correlate with diurnal changes in photosynthesis (Owen-Smith and Goodall, 2014). Furthermore, many important bison life-history events recur in seasonal patterns (e.g., breeding and calving), and may partially explain some of our results (Lott, 2002). It is possible that our results represent a species-wide response to season and time of day, but more data from the broader North American population are needed to confirm that hypothesis.

Differences between daytime and nighttime movement probability and distances may represent a response to temperature fluctuations during those seasons. Specifically, we observed that the differences between daytime and nighttime movement distances and probabilities were the lowest during the summer than any other season. To regulate their internal temperature during particularly warm times of the year, bison may seek out thermal refugia where operative temperatures are lower than the surrounding environment (Allred et al., 2013). However, some ungulates also may move at different times throughout the diurnal cycle to offset the effects of thermal stress (Owen-Smith, 1998; Owen-Smith and Goodall, 2014), electing to move in the cooler parts of the diurnal cycle rather than the heat of the day. Therefore, our observed movements may be partially explained by bison moving at times that minimize their exposure to unfavorable weather patterns, and should be considered directly in future studies.

Bison movements, as with all ungulates, are undoubtedly influenced by plant phenology (Merkle et al., 2016). Plant phenology changes heterogeneously across space and time, being significantly affected by precipitation, elevation, temperature, light, and also by various land management actions (e.g. fire, grazing, etc.; Aikens et al., 2017; Bischof et al., 2012; Geremia et al., 2019). Therefore, the relationship between ungulate movement and plant phenology is nearly infinitely complex, and are often highly variable between individuals within a non-migratory ungulate population (Mueller et al., 2011; van Beest et al., 2013). Due to the complex, and data-intensive nature of time-series phenological analyses of ungulate movement, our study helps put into focus points in time when phenology may be driving seasonal differences in bison movements. For example, we show that bison move less often and shorter distances in the winter compared to other seasons. Future research pairing each 12-minute movement with daily Normalized Difference Vegetation Index (NDVI) values during the autumn and winter would offer insight into how any seasonal changes in greenness might be driving those movements.

Our study represents the first assessment of seasonal and diurnal bison movement using fine resolution GPS data from multiple herds on multiple large complex landscapes. The bulk of bison movement studies are focused on how landscape patterns influence where bison are likely to move (e.g. Geremia et al., 2019; Kohl et al., 2013). We know of no other studies analyzing bison movement through time, irrespective of landscape (e.g. slope and elevation) or resource selection patterns (e.g. foraging area, home-ranges, etc.). Therefore, our study is intended to be a starting point in addressing why seasonal and diurnal rhythms affect the frequency and magnitude of bison movements. Future studies should use more complex methods of landscape analysis (including plant phenology metrics matched with each movement) to zero-in on the mechanisms that might be driving the seasonal and diurnal bison movements we describe here. The results of movement studies are likely to change with scale (Northrup et al., 2016; Rivrud et al., 2010a) and landscape complexity (Crone et al., 2019). Ungulate movement is also significantly affected by weather (Rivrud et al., 2010a; Schmidt et al., 2016), and is predicted to change drastically in response to climate shifts resulting from the Anthropocene (Craine et al., 2015; Dirzo et al., 2014). Therefore, future studies should also continue to uncover the interactions between scale, landscape complexity, and weather on ungulate movement patterns. If we are to conserve iconic species like bison into the future, it is essential that researchers continue to close gaps in our basic understanding of ungulate movement to buffer against future change.

Table 1.1: The total area (ha), elevation (m), range of slope (%), fire management, dominant plant community, average forage productivity (kg/ha), forage productivity range (kg/ha), and average annual rainfall (cm) between the Tallgrass Prairie Preserve (TPP) and Wichita Mountains Wildlife Refuge (WMWR). We define large prescribed (Rx) fire as single fires that cover the majority (or sometimes all) of the landscape. We refer to patch-burns as being small (far less than half the area of a landscape) fires that are heterogeneously applied across a landscape through time (see Fuhlendorf et al. 2009). Average annual rainfall was procured from the Foraker and Medicine Park Mesonet stations (https://www.mesonet.org) at the TPP and WMWR respectively, and represents the conditions during the years 2008 - 2012. Forage productivity and plant community metrics were obtained from the United States Department of Agriculture's Web Soil Survey (https://websoilsurvey.nrcs.usda.gov), and represents total available dry forage under normal conditions.

Site	Total Area (ha)	Elevation min-max (m)	Slope min-max (%)	Fire Management	Dominant Plant Community	Average Forage Productivity (kg/ha)	Forage Productivity min-max (kg/ha)	Average Annual Rainfall (cm)
TPP	9,400	244-335	0-45	Patch-Burn	Tallgrass Prairie	4,231	1,267-9,021	95
WMWR	23,885	422-755	0-50	Large Rx Fire	Mixed-grass prairie	2,874	336-6,888	62

Table 1.2: Model comparison tables where delta-AIC values and degrees of freedom are reported for each combination of model parameters we tested. Models were fit to predict movement (Binomial) or movement distances. We set Individual as the random intercept effect for all of our models.

Binomial

Model Parameters	ΔAIC	df
Site*Season + Season*TOD	0.0	13
Site*Time of Day + Season*TOD	197.2	11
Season*TOD	247.8	9
Site*TOD	2,508.9	5
Season + TOD	2,619.0	6
TOD	2,682.8	3
Site + TOD	2,684.5	4
Site * Season	27,052.8	9
Season	27,353.5	5
Site + Season	27,355.0	6
Null	28,086.8	2
Site	28,087.9	3

Movement Distance

Model Parameters	ΔAIC	df
Site*Season + Season*TOD	0.0	14
Site*TOD + Season*TOD	1,194.1	12
Season*TOD	1,335.9	10
Season + TOD	5,934.5	7
Site*TOD	21,712.3	6
Site + TOD	22,439.0	5
Time of Day	22,452.0	4
Site*Season	31,630.0	10
Site + Season	32,733.8	7
Season	32,735.4	6
Site	49,013.9	4
Null	49,024.5	3

Table 1.3: Summary table showing the total GPS observations collected, mean movement distance (Mean Step Length), and standard deviation in movement distances (SD) across each season (spring, summer, autumn, and winter) and time of day (day and night) for our bison movement dataset.

Tallgrass Prairie Preserve (TPP)

Season	Time of Day	Total GPS Observations	Mean Step Length (m)	SD
spring	day	65,530	72.8	116.2
spring	night	54,224	44.1	102.8
summer	day	68,985	78.0	146.3
summer	night	48,634	61.9	114.7
autumn	day	27,638	80.4	114.9
autumn	night	27,545	42.1	87.2
winter	day	37,374	54.4	109.5
winter	night	51,708	19.6	43.2

Wichita Mountains Wildlife Refuge (WMWR)

Season	Time of Day	Total GPS Observations	Mean Step Length (m)	SD
spring	day	30,146	74.1	110.1
spring	night	25,816	37.4	82.0
summer	day	18,795	74.0	114.6
summer	night	13,032	42.5	85.4
autumn	day	10,014	65.7	92.0
autumn	night	13,525	27.3	68.1
winter	day	17,789	57.4	91.3
winter	night	24,493	23.4	63.1

Figure 1.1: Relative movement frequencies across all four seasons (spring, summer, autumn, and winter) and our two sites (TPP and WMWR). Small points represent mean movement frequency for each individual, and large points represent the mean movement frequency across all individuals. Data is from the two bison herds we used in this study.

Figure 1.2: Observed movement frequencies across all four seasons (spring, summer, autumn, and winter) and two times of day (day and night). Data is from two bison herds in the Great Plains, and was collected from 2008-2010 and 2010-2012 respectively. Smaller points represent the mean movement frequency for each individual, and larger points represent the mean movement frequency across all individuals.

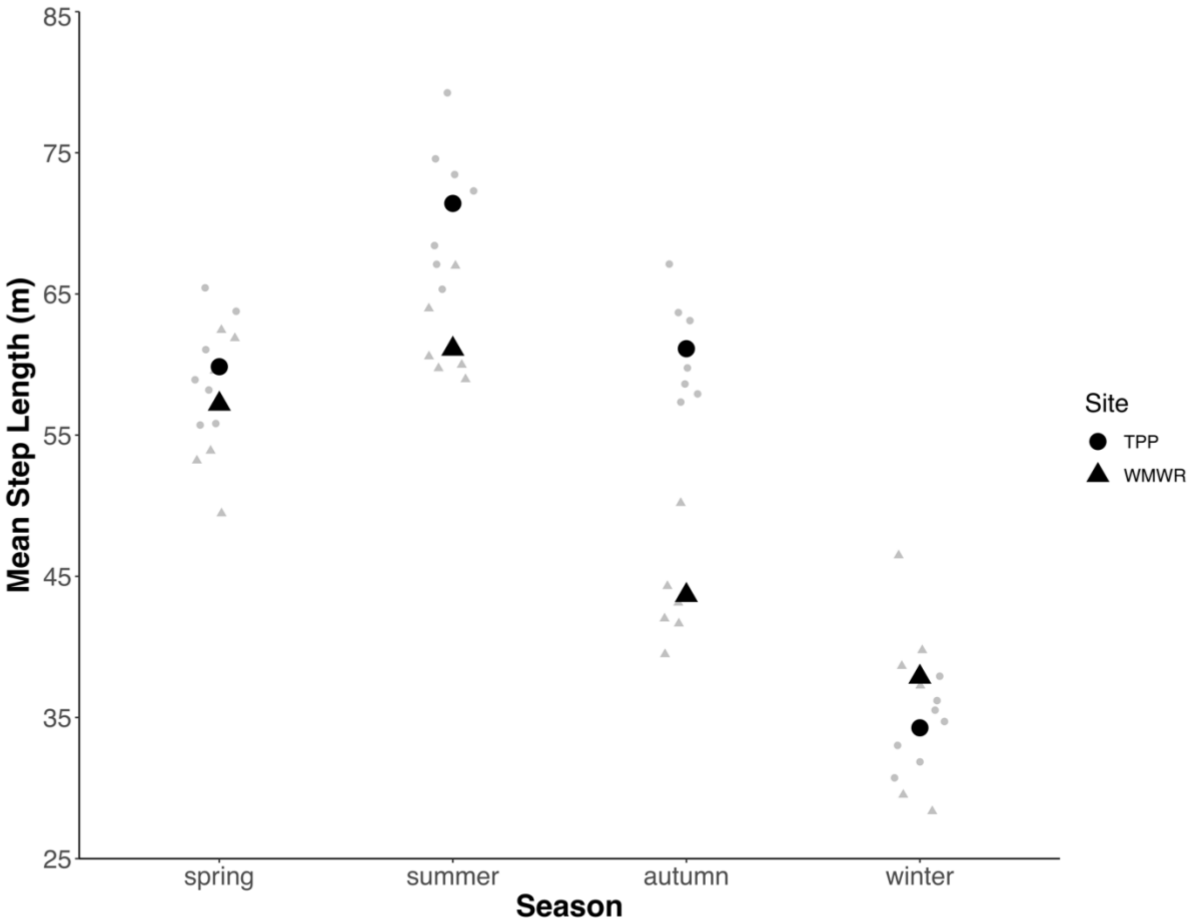

Figure 1.3: Mean bison step length distances (m) by season (spring, summer, autumn, and winter) and between our two sites in the Great Plains – the Tallgrass Prairie Preserve (TPP) and the Wichita Mountains Wildlife Refuge (WMWR). Small points represent mean step lengths (m) for each individual, and large points represent the mean step length (m) across all individuals. Step lengths represent the total distance moved during a 12-minute period. Total GPS points we recorded for spring, summer, autumn, and winter were: 175,816; 151,428; 82,904; and 144,823 respectively.

Figure 1.4: Mean bison step length distances (m) by season (spring, summer, autumn, and winter) and time of day (Day and Night). Data is from two bison herds in the Great Plains, and was collected from 2008-2010 and 2010-2012 respectively. Smaller points represent the mean movement frequency for each individual, and larger points represent the mean movement frequency across all individuals. Total GPS points we recorded for spring, summer, autumn, and winter were: 175,816; 151,428; 82,904; and 144,823, respectively.

CHAPTER II

BISON MOVEMENTS CHANGE WITH WEATHER: IMPLICATIONS FOR THEIR CONTINUED CONSERVATION IN THE ANTHROPOCENE

Abstract

Animal movement patterns are significantly affected by the complex interactions between biotic and abiotic landscape conditions, and will be altered by weather variability associated with future climate change. Some animals, like the American plains bison (*Bison bison* L.; hereafter, bison), are considered keystone species, and their response to climate and weather variability may alter grassland structure and biodiversity patterns. Many movement studies have been focused on point-pattern analyses (e.g., resource-selection), revealing where large ungulates, like bison, move. However, much about when or why animals move remains shrouded, including ungulate movement responses to climate. We utilized 12-minute GPS bison movement data from two of the largest herds in North America to explore how movement distance is affected by fine-scale weather patterns and drought. We fit bison movement response to weather and drought parameters using generalized additive mixed-models to determine which parameters most affected average movement distance. How far bison move was strongly affected by weather, but was most strongly affected by air temperature, and rainfall. Notably, bison moved further during hotter and drier times than those that were cooler with abundant rainfall. Moreover, short-term drought (as indicated by shallow soil moisture metrics) was a stronger predictor of fine-scale bison movement distance than other drought measures used in this study. As climate and weather patterns shift across their current range, bison movements will be affected, likely complicating attempts to contain them within allotted conservation areas, and potentially escalating ongoing conflict in the Great Plains. Changes in ungulate movement resulting from sustained climate changes could be consequential for future grassland biodiversity (e.g., altered herbivory disturbance patterns known to be critical to biodiversity maintenance), and conservation efforts will need to adapt.

Keywords: ungulates, landscape, grasslands, climate change, movement ecology, conservation, weather variability

Introduction

The movement patterns of many large ungulates are entwined with the cyclical rhythms of their environment (e.g., seasonal patterns of vegetation phenology), which are in-part driven by climate and weather (Bruggeman et al., 2008; McMillan et al., 2021). Anthropogenic climate change is predicted to alter global weather patterns (Cai et al., 2014), and carries implications for future species conservation efforts (Stenseth et al., 2002; Thomas, 2010). Many ungulates are strongly influenced by climate patterns (Augustine, 2010), often moving long-distances to follow weather-induced changes in forage quality (Fryxell and Sinclair, 1988; Holdo et al., 2009; Mueller et al., 2008). However, due to anthropogenic pressures, some large ungulates, like American plains bison (*Bison bison* L.) and elk (*Cervus elaphus* L.), have mostly become restricted to roaming small, highly regulated conservation areas relative to the landscapes they once inhabited (Frair et al., 2005; Geremia et al., 2019). While many studies have addressed how ungulate habitat selection changes in response to physical landscape features (e.g., phenology, topography, roads), relatively few have attempted to address how their movement is affected by weather or climate dynamics (McMillan et al., 2021). It is likely that many large ungulates will experience climate change-induced range boundary shifts (Thomas, 2010), which further complicates ongoing maintenance efforts for many species already restricted to small conservation areas due to human encroachment. Therefore, understanding how ungulates respond to weather and prolonged climate change will be critical as we rethink global conservation efforts and priorities in the face of uncertainty during the Anthropocene.

The American plains bison is a large ungulate grazer that historically roamed nearly all of North America, spanning the entire Great Plains and portions of the eastern and western regions of the continent (Hall, 1981). Historical movement patterns of bison across North America were loosely described by early European and American explorers (Hornaday, 1889; Shaw, 1995), but actual movement patterns of individuals and populations is speculative at best. Since their near extinction in the late 19th and early 20th century, most bison have been relegated to small, restricted, and structurally homogenous landscapes that are quite different from the expansive, heterogeneous landscapes they once roamed (Fuhlendorf et al., 2018; Sanderson et al., 2008). Therefore, studies of extant bison have been mostly limited to single small herds, or relatively homogenous landscapes that are managed under an agricultural paradigm (e.g., landscapes managed under a paradigm meant to maximize sustainable forage production for livestock; generally with light to moderate disturbance and climax plant community dominance as management objectives; Fuhlendorf et al., 2012; McMillan et al., 2021). Although bison are considered by some as an integral, keystone player in grassland ecosystem function (Knapp et al., 1999; McMillan et al., 2019), these effects (e.g., plant community differences in bison grazed grasslands versus those where they are excluded, creation of ephemeral habitat for amphibians and invertebrates through wallowing behaviors) may be highly context-specific, and confounded by management (Fuhlendorf et al., 2018). It is likely that bison indeed played a role in shaping

North American grassland ecosystems historically, but that role was mediated by interactions among many environmental variables (e.g., fire, drought, etc.). Highly variable climate and weather patterns influence the conditions and resources that are characteristic of grassland landscapes, and are central factors that influence animal movement.

Much of the bison movement literature is limited to point-pattern investigation (e.g., resource-selection) in which researchers set out to determine how habitat configuration and composition affect where bison move on the landscape. Very few studies have attempted to address how bison move through space irrespective of where they are on the physical landscape (McMillan et al., 2021). Moreover, although weather may influence the energetic costs of movement (e.g., increased wind speed being linked to an increased energetic cost of movement) (Halsey, 2016), few studies have confirmed or described the effect of weather on movement for many species of conservation interest. In spite of the many conservation actions being taken regarding the American plains bison (Fuhlendorf et al., 2018; McMillan et al., 2019), there is limited understanding of the importance of weather on their movement (McMillan et al., 2021). For example, with the exception of habitat and forage preferences (Allred et al., 2013; Craine et al., 2015), how bison movements are affected by climate and weather extremes, including drought, remains unknown. Bison have also shown seasonal movement patterns that may be driven, in-part, by climate and weather (McMillan et al., 2021). Understanding the role of weather patterns in determining large ungulate movement will provide the baseline to evaluate information on movements associated with conservation activities, as well as address some long-held anecdotal hypotheses surrounding their movement (Bowyer, 1981; e.g., bison move more when winds are out of the north). Further, growing social conflict surrounding ungulate movement has created tension between many agricultural production and conservation actions (Cleveland et al., 2012; Jachowski et al., 2014; Plumb et al., 2009; e.g., competition with livestock for available forage, destruction of cultivated agricultural products, destruction of infrastructure – namely, fences – and increased disease transmission) that are likely going to get worse with changing climate. Given increasing social conflict (Plumb et al., 2009) and landscape fragmentation, how these (and other) large and important herbivores respond to climate may determine the feasibility of their continued conservation throughout the Anthropocene. Moreover, how large ungulates respond to climate change may require a major rethinking of current and future conservation strategies to mitigate against future uncertainty or loss of functionally important species (e.g., keystone species).

We analyzed a robust dataset from two of the largest bison herds in North America, i.e. the Wichita Mountains Wildlife Refuge and the Tallgrass Prairie Preserve, to investigate how bison movement is affected by weather patterns across large complex landscapes. Weather is hypothesized to drive bison movement directly through physiological stress (Allred et al., 2013), as well as indirectly by altering the quality and quantity of resources needed for survival and maintenance (McMillan et al., 2021; Sage and Kubien, 2007). Movement distance (i.e., displacement or step length) is a powerful primary movement signal that allows researchers to explore possible animal behavioral responses to the external environment (Edelhoff et al., 2016), including weather. Further, measuring how far bison move in response to weather may have direct implications for their future conservation, as conflict surrounding bison increasingly includes the ability (or inability) to contain them inside allotted grazing areas (Davenport, 2018; Plumb et al., 2009). Therefore, we set out to determine how weather (i.e., wind speed, wind direction, relative humidity, rainfall, air temperature, solar radiation) as well as drought affect fine-scale bison movement distances (i.e., a primary path-signal) across two large grassland landscapes.

Methods

Study Areas

The data we used in our study were collected across two sites in Oklahoma, USA that vary considerably in their topography, vegetation, and climate: The Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve (hereafter, Tallgrass Prairie Preserve) and the United States Fish and Wildlife Service's Wichita Mountains Wildlife Refuge (Table 2.1; McMillan et al., 2021). The Tallgrass Prairie Preserve is divided into two distinct units based on the dominant grazer (cattle or bison), and our study focused on data collected in the 9,400-ha bison unit where approximately 2,500 bison are allowed to freely graze year-long. Most of the Tallgrass Prairie Preserve is managed with fire under the patch-burning management paradigm that is focused on restoring structural heterogeneity on the landscape (Hamilton, 2007). Fire is applied at various times throughout the year in the Tallgrass Prairie Preserve's bison unit to mimic historic fire regimes (Hamilton, 2007).

At 23,884-ha, the Wichita Mountains Wildlife Refuge is made up of several ecosystems that vary with elevation (McMillan et al., 2021), but the grasslands occurring throughout the refuge are characterized as mixed-grass prairie. Precipitation is much lower on average, but temperatures are similar to the Tallgrass Prairie Preserve (Table 2.1; Brock et al., 1994; McPherson et al., 2007). The Wichita Mountains Wildlife Refuge is actively managed with prescribed fire and grazing, although unlike the Tallgrass Prairie Preserve, approximately 650 bison and 220 longhorn cattle graze jointly across most of the refuge.

Data Collection

For this study, we utilized GPS-telemetry data collected by The Nature Conservancy and the United States Fish and Wildlife Service from 2008 – 2012 (Allred et al., 2011a; McMillan et al., 2021). GPS data were collected from seven female individuals per year from the Tallgrass

Prairie Preserve from November 2008 – November 2011 (i.e., via The Nature Conservancy), and six female individuals per year from the Wichita Mountains Wildlife Refuge from November 2010 – July 2012 (i.e., via the United States Fish and Wildlife Service; 33 individual bison total). Collar location data were recorded at 12 minute intervals for all individuals. From 2008 – 2010, patches within the Tallgrass Prairie Preserve's bison unit were annually burned and the unit was moderately stocked across a 9,400-ha unit (McMillan et al., 2021). From 2010 to 2012, the Wichita Mountains Wildlife Refuge did not have a fixed burn schedule and was lightly stocked with bison and longhorn cattle (McMillan et al., 2021). GPS data was differentially corrected prior to analysis, using data from nearby base stations (Allred et al., 2011a).

To analyze how bison movements are affected by weather, we paired each 12-minute movement with the corresponding on-site weather condition. We specifically used data from the Foraker and Medicine Park Mesonet weather stations (Brock et al., 1994; McPherson et al., 2007). We collected 2-meter air temperature, 10-meter wind speed, wind direction, relative humidity, solar radiation, 24-hour rainfall accumulation, and daily calibrated soil temperature (5 and 25 cm depth) data from November 2008 – November 2010 and November 2010 – November 2012 for the Foraker and Medicine Park stations respectively. We used calibrated soil temperature data to calculate daily fractional water index (Illston et al., 2008) values as a way to assess drought conditions at each site as well.

Data Analysis

To investigate how climate affects bison movement patterns we calculated movement distance from our GPS data, and matched them with corresponding weather data collected at each site. We used the package "amt" in R version 4.1.2 (R Core Team, 2021; Signer et al., 2019) to clean and process all of our GPS-data prior to analysis. We calculated the distance travelled for each 12-minute movement in our processed dataset using the function step_length (Signer et al., 2019). With the exception of rainfall and soil temperature data (each reported as daily summaries), all other primary weather metrics were recorded in 5-minute intervals. We paired each movement with the nearest 5-minute weather observation to overcome the timing offset between the movement and weather data used in this study.

We explored the relationships between bison movement and each weather metric individually, as well as all possible combinations using generalized additive mixed models – including linear and smoothed predictor combinations. We also explored relationships between drought (via fractional water index) and bison movement using the same approach. We fit smoothed predictors (i.e., 2-meter air temperature, 10-meter wind speed, relative humidity, solar radiation, 24-hour rainfall accumulation, and daily calibrated soil temperature) in our generalized additive mixed models using a cubic spline smoothing basis. Since we treated wind direction as categorical, it was always fit as a parametric (i.e., unsmoothed linear) predictor. All weather parameters were checked for correlation prior to analyses, and no strong correlations were detected among them. All models were fit following a Gamma distribution with a log-link function. We accounted for potential variation among individuals, as well as repeated measures for any one individual and across sites, by using the individual ID nested within site as a random intercept in all models. Since we utilized fine-resolution GPS movement data, our observed bison movements were moderately autocorrelated in time. We treated each uninterrupted track in our movement dataset as an ordered time-series (i.e., treated each burst of movement as an individual autoregression event), and added first-order autoregression (i.e., AR(1)) terms to all of our fitted models using the package "mgcv" in the program R (Wood and Wood, 2015; Wood, 2017) to correct for temporal autocorrelation. We then ranked model fits for each analysis (i.e., weather and drought) using corrected Akaike information criterion (AICc). Although the two study areas in this study differ in topography, precipitation, and plant community structure (Table 2.1), previous research suggests that the two sites do not differ with respect to bison movement through time (McMillan et al., 2021).

Results

We analyzed 715,344 total 12-minute movements from 33 female bison, averaging approximately 21,677 12-minute movements per individual, across two sites in Oklahoma. Overall, mean bison movement distance across all individuals and years was 56.9 m per 12-minute movement path (SE = 0.1 m) with approximately 28% of the total observed movements being longer than the mean.

Response to Weather

Air temperature and solar radiation had a strong influence on fine-scale (12-minute) GPS movements of bison across two large, intact grasslands in the Southern Great Plains. Of the variables examined, air-temperature had the strongest effect of any single weather parameter we tested (Figure 2.1), and was included in all of the top models (Table 2.2). Average bison movements were shortest when air temperatures were below 0℃ (Figure 2.1). Mean movement distances increased from 0℃ to their longest at 30℃, and declined or leveled off when temperatures were greater than 30℃ (Figure 2.1). About 81% (431,417) of the total observations were distributed between 0℃ and 30℃. At the temperature extremes, 10% (53,267) of the total observations were from times when air temperature was below 0℃, and 9% (50,519) were from times above 30℃. Observed temperatures across the two sites overall ranged from -21.3℃ to 44.3℃.

The top model in our analysis also included 10-meter wind speed, wind direction, daily rainfall accumulation, relative humidity, and solar radiation (Table 2.2). Solar radiation only had a strong effect on bison movement distances at moderate to high (500 – 1,000 Wm^{-2}) levels, as we found that lower solar radiation levels (< 500 Wm^{-2}) had virtually no distinguishable effect on bison movement distance (Figure 2.1). The bison also tended to only be affected by relative humidity during very dry conditions, being seemingly unaffected during conditions above 25% relative humidity (Figure 2.1). Mean bison movement distances varied with daily rainfall accumulation, with a bimodal relationship between 0 and 5 cm of accumulated daily rainfall (Figure 2.1). Although they were included in the top model (i.e., likely have a statistically significant relationship with movement distance), we could not find a distinguishable relationship between 10-meter wind speed or wind direction and mean bison movement distance (Figure 2.1).

Response to Drought

We calculated daily fractional water index (Illston et al., 2008) values using calibrated soil moisture data from weather stations near each study site, and paired them with corresponding bison movements to analyze how distance moved might be affected by measures of drought. We found that bison movement was best predicted by changes in 5-cm fractional water index (i.e., an index of soil moisture conditions) compared to measurements deeper in the soil profile (Table 2.3). Mean bison movement distance was inversely related to fractional water index, being that bison movement was longer during periods of drought (fractional water index values less than 0.4) than when soils were saturated (fractional water index values greater than 0.7). We found that mean movement distances were highest when 5 cm fractional water index values were between 0.00 and 0.40 ($\bar{x}$ = 67.9 m, SD = 10.8), and declined when above 0.8 ($\bar{x}$ = 52.4 m, SD = 11.2; Figure 2.2).

Discussion

This study represents the most robust analysis to date showing that fine-scale, non-migratory ungulate movements, in our case, those from American plains bison, may be strongly dependent upon weather. When confronted with ambient physiological stress, all ungulates are faced with two choices to mitigate that stress: (1) move to a new place on the landscape where the stress is relieved or avoided; or (2) acclimate to the current condition. During times of excessive heat, we show that bison may roam longer distances, possibly in search of forage or structural cover to meet increased physiological needs. Excessive heat specifically has a direct effect on where bison move on the landscape as well, seeking out thermal refugia – often riparian areas – to escape extreme heat (>39°C; Allred et al., 2013). Air temperature has strong direct (via physiological effects, through increased energetic and nutrient demands; Martin and Barboza, 2020) and indirect (e.g., temperature-driven changes in forage quality; Sage and Kubien, 2007) effects on where and how many other ungulates move across landscapes as well (Schmidt et al., 2016; van Beest et al., 2013, 2012). Moreover, that bison movements are dependent upon weather variables like air temperature may explain, in-part, a mechanism driving observed seasonal movement patterns (McMillan et al., 2021). The effect that air temperature has on animal movement may also be significantly affected by the concurrent solar radiation conditions (i.e., the solar energy available to be absorbed by an animal's skin or fur; Kay, 1997), further supporting a likely complex interaction between weather patterns and animal movement. Seasonal changes in resource quality, quantity, and spatial distribution undoubtedly also explain some of our observed bison movement data. However, it is unlikely that seasonal variability in resources alone describes fine-scale bison movements across our two sites given the strength of some weather parameters (e.g., air temperature) on their movement decisions. Our results add to a growing body of evidence supporting that climate and weather not only directly affect where animals move, but also how they move across landscapes (Rivrud et al., 2010b; Schmidt et al., 2016; van Beest et al., 2013, 2011). Future research should continue to disentangle how weather interacts with other environmental variables through time to influence bison behavior.

Although climate dynamics affect many aspects of conservation landscapes (e.g., patterns of forage quality and quantity, water availability, and habitat structure; Kulmatiski and Beard, 2013; Thomas, 2010), previous analyses of ungulate movement have largely been skewed toward addressing how physical landscape features (e.g., topography, forage distribution, human structures, etc.) alone influence movement, often ignoring climate or weather. Our results add to a growing line of evidence suggesting that ungulate movement patterns are affected by more than patterns of forage distribution and quality alone (Allred et al., 2013; Herfindal et al., 2019; van Beest et al., 2012), and include the interactive effects of weather variables on animal movement. Weather-driven alterations in ungulate movement have the potential to affect landscape structure and function via changes in disturbance frequency, timing, and intensity. Changes in herbivory-vegetation feedbacks, for example, can have cascading effects relevant to ecosystem function and conservation (e.g. increased fire threat, woody plant encroachment, etc.; Fuhlendorf and Engle, 2001; Werner et al., 2020). Alterations to these feedbacks as a result of climate change may, therefore, be consequential in the success, or failure, of current and future conservation efforts.

Prior to wide human expansion, when extreme drought or inhospitable weather patterns occurred across expansive landscapes, large ungulates would have been able to freely move great distances in search of more hospitable conditions. However, human expansion across the globe has relegated many large ungulate species to relatively small, homogenously managed, fenced landscapes that are often privately owned. As we move through the Anthropocene, changes in climate are predicted to accelerate faster than the ability of many species to adapt, potentially resulting in shifts in species distributions (Cahill et al., 2013; Thomas, 2010) or extinction (Duncan et al., 2012). However, for large ungulates (like bison) that are adapted to a wide range of ecosystems, the threat may be more related to restrictions to movement (e.g., fragmentation, urbanization, etc.), as long distance movements to avoid or moderate weather extremes are not an option. Even in vast landscapes like Yellowstone National Park (899,116 ha) where a considerable portion of the nearly 5,000 resident bison annually leave the park, such movements are restricted or discouraged through culling or hazing (Plumb et al., 2009). Similar conflicts surrounding movement exist for other ungulates globally, including elk (Frair et al., 2005) and elephants in Africa (*Loxodonta africana* Blumenbach) and Asia (*Elephas maximus* L.; Shaffer et al., 2019). This further highlights the complexity of developing conservation efforts to mitigate climate change impacts on large ungulates. Our results suggest that facilitating increased movement may be key to sustaining bison and other large ungulates in the future, even across vast landscapes (e.g., Yellowstone National Park or Kruger National Park), as they will likely move further out of allotted areas as temperatures warm, and droughts become more frequent, severe, and longer lasting. Many of the world's existing large conservation areas are arranged, or managed, in ways that harbor very little ecological resiliency during times of change (Fuhlendorf et al., 2018; Holling and Meffe, 1996). Moreover, as new ambitious rewilding and restoration efforts grow (Fuhlendorf et al., 2018), few include actions based around increasing ecological resiliency (Holling and Meffe, 1996) through process, as well as species, restoration. Weathering the effects of climate change, therefore, may ultimately mean rethinking the size, orientation, and management of new and existing conservation areas so as to better meet the shifting needs of their resident ungulate populations.

Table 2.1: The total area (ha), elevation (m), typical topography, dominant plant community, range in daily average temperature (°C), and average annual rainfall (cm) between the Joseph H. Williams Tallgrass Prairie Preserve and Wichita Mountains Wildlife Refuge. Daily average temperature and average annual rainfall were obtained from the Foraker and Medicine Park Mesonet stations (https://www.mesonet.org) at the two sites respectively, and represent conditions during the years 2008 - 2012.

Site	**Total Area (ha)**	**Elevation min-max (m)**	**Topography**	**Dominant Plant Community**	**Daily Average Temperature min-max (°C)**	**Average Annual Rainfall (cm)**
Joseph H. Williams Tallgrass Prairie Preserve	9,400	244 – 335	Rolling Hills	Tallgrass Prairie	-14.0 – 32.0	95
Wichita Mountains Wildlife Refuge	23,885	422 – 755	Steep Mountains and Valleys	Mixed-grass prairie	-12.5 – 36.2	62

Table 2.2: AICc table showing the top seven competing General Additive Mixed Models explaining the effect of weather on bison movement distances (i.e., step lengths). Movement data was collected every 12-minutes from November 2008 – November 2010 and November 2010 – November 2012 at the Joseph H. Williams Tallgrass Prairie Preserve and the Wichita Mountains Wildlife Refuge, respectively. All were fit with individual ID as a random effect to account for variability present among individuals, as well as repeated movement measures for each individual. Model parameters marked with an asterisk were fit as linear predictors (i.e., were not fit with a smoother, and treated as parametric). Otherwise, model parameters were fit with a cubic spline smoothing basis.

Model	**ΔAIC$_c$**	**AIC$_c$ Weight**
Air Temperature + Wind Speed + Wind Direction* + Daily Rainfall Total + Relative Humidity + Solar Radiation	0.0	1.0
Air Temperature + Daily Rainfall + Solar Radiation	659.0	< 0.001
Air Temperature + Wind Direction* + Solar Radiation	685.6	< 0.001
Air Temperature + Relative Humidity + Solar Radiation	934.7	< 0.001
Air Temperature + Wind Speed + Solar Radiation	5087.3	< 0.001
Air Temperature + Solar Radiation	5702.0	< 0.001
Air Temperature + Wind Direction* + Daily Rainfall	5942.3	< 0.001

Table 2.3: AICc table showing competing General Additive Mixed Models explaining the effect of drought (i.e., using fractional water index, or FWI) on bison movement distances (i.e., step lengths). Movement data was collected every 12-minutes from November 2008 – November 2010 and November 2010 – November 2012 at the Joseph H. Williams Tallgrass Prairie Preserve and the Wichita Mountains Wildlife Refuge, respectively. FWI was calculated using daily soil moisture data from the two sites. All were fit with individual ID as a random effect to account for variability present among individuals, as well as repeated movement measures for each individual. Model parameters marked with an asterisk were fit as linear predictors. Otherwise, model parameters were fit with a cubic spline smoothing basis.

Model	**ΔAIC_c**	**AIC_c Weight**
5-cm FWI	0.0	1.0
5-cm FWI*	1816.7	< 0.001
25-cm FWI	2406.8	< 0.001
25-cm FWI*	3375.7	< 0.001
Null	7383.6	< 0.001

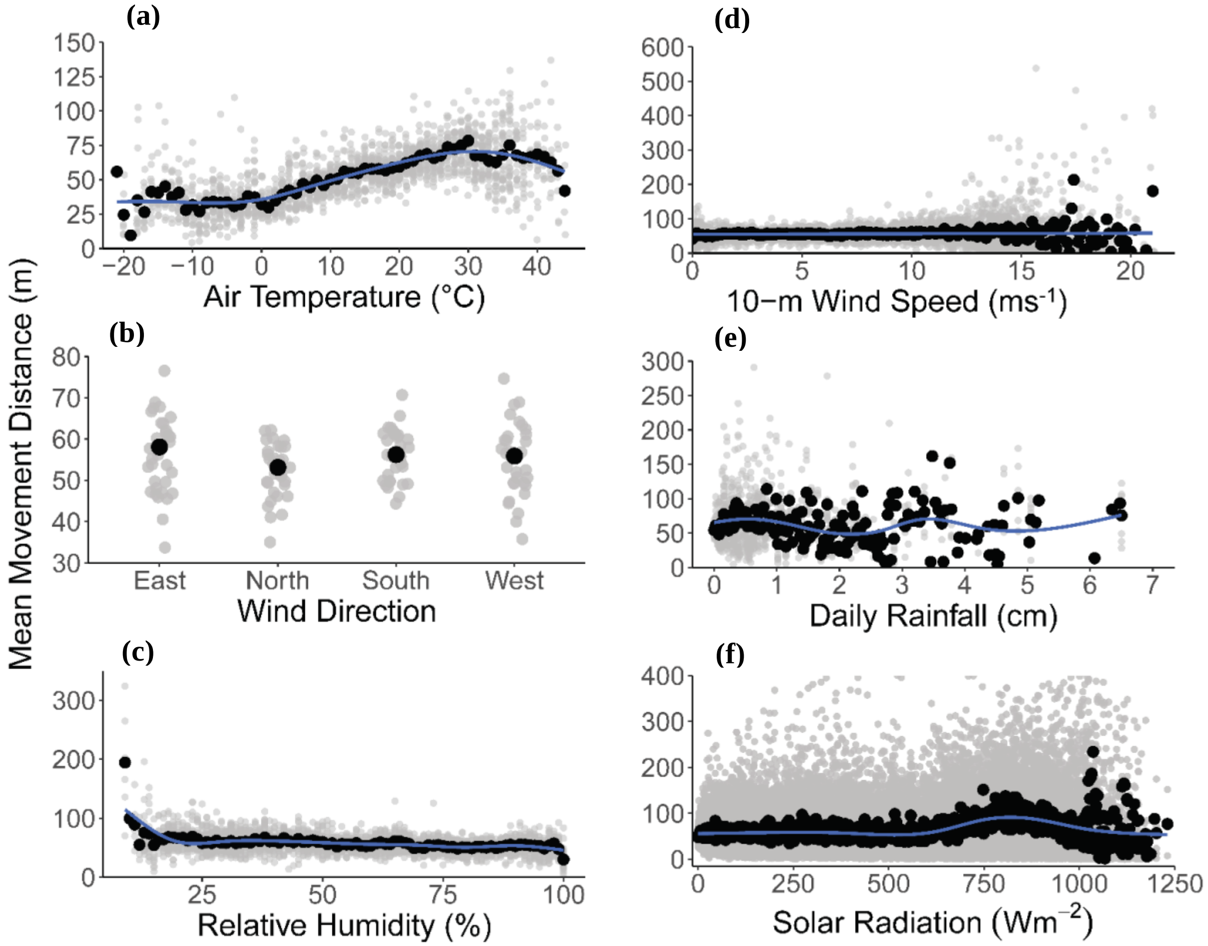

Figure 2.1: Average distance moved (m) by bison every 12-minutes relative to concurrent **(a)** air temperature (°C), **(b)** wind direction, **(c)** relative humidity (%), **(d)** wind speed measured at 10 m height (ms^{-1}), **(e)** daily total rainfall (cm), and **(f)** solar radiation (Wm^{-2}) at the Joseph H. Williams Tallgrass Prairie Preserve and the Wichita Mountains Wildlife Refuge from November 2008 – November 2010 and November 2010 – November 2012, respectively. Small grey points represent the mean movement distance travelled for each of our 33 individuals at each weather measurement, and large black points represent the mean movement distance travelled across all individuals. Lines fitted using generalized additive modelling with a cubic spline smoothing basis.

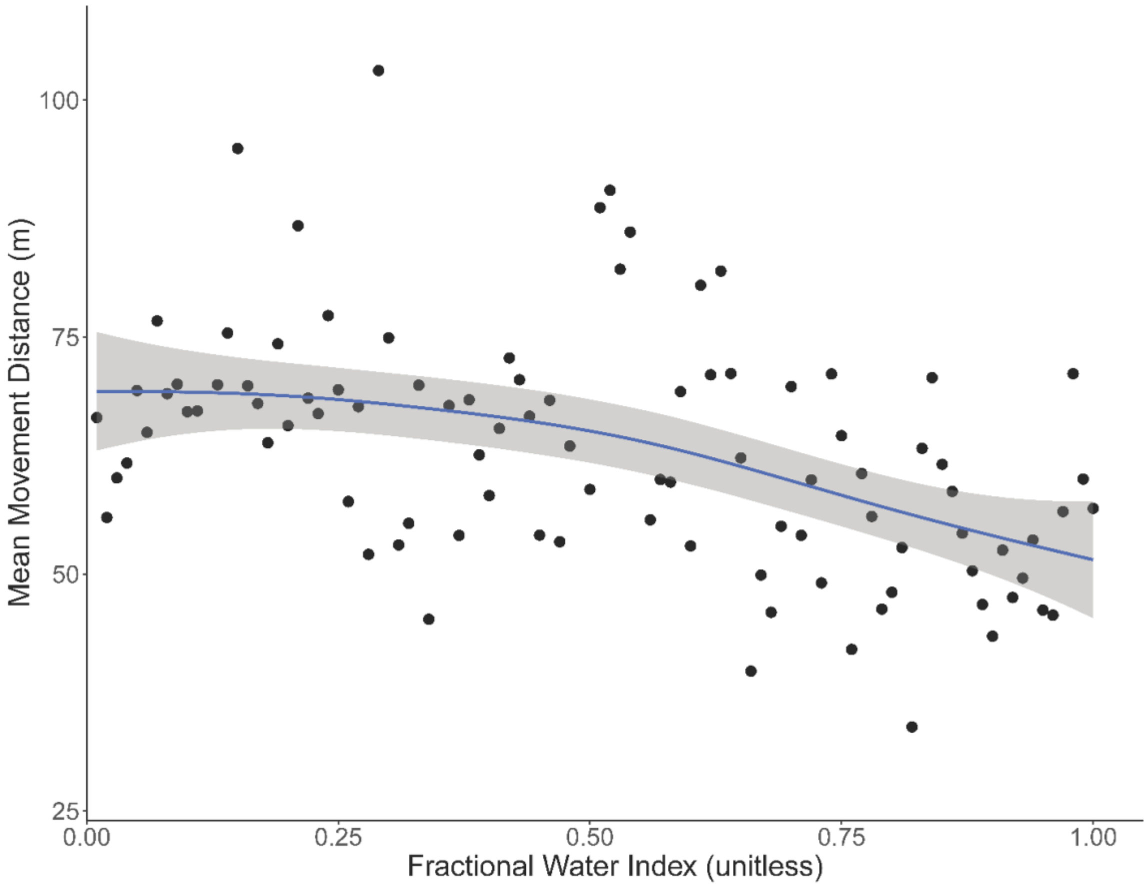

Figure 2.2: The relationship between mean bison movement distance (m) and fractional water index measured at 5 cm soil depth. Fractional water index values correspond to soil moisture, ranging from 0 – 1, representing powdery dry and fully saturated soils respectively. Points represent mean movement distances across all individuals and sites. Line was fitted using a generalized additive model with a cubic spline smoothing basis. Shaded area represents a 95% confidence interval around the fitted mean. Data represents conditions from both the Joseph H. Williams Tallgrass Prairie Preserve and the Wichita Mountains Wildlife Refuge from November 2008 – November 2010 and November 2010 – November 2012, respectively.

CHAPTER III

DOES FIRE AND HERBICIDE BENEFIT CATTLE PRODUCTION IN INVADED GRASSLAND LANDSCAPES?

Abstract

Invasive species management is promoted as a general practice to maintain rangeland biodiversity and mitigate livestock performance losses stemming from invasive-species effects (e.g., competitive exclusion of palatable forages). It is hypothesized that altering fire-timing (e.g., moving from early to late-growing season burning) or integrating herbicide application into fire management regimes may lead to more successful reduction of certain invasive species without negatively affecting livestock performance. However, large-scale, replicated experimental evidence linking invasive species abundance or management practices to cattle performance is mostly lacking across grasslands. We manipulated eight large (333 – 766 ha) pastures managed with fire and grazing (i.e., pyric herbivory) to test how growing (i.e., August-September) and dormant (i.e., March-April) season fires, herbicide application, or invasive species abundance (namely *Lespedeza cuneata*) affected yearling cattle performance – i.e., per head weight gain – from 2018 to 2020. We found that yearling cattle gained significantly less weight in landscapes burned during the growing season, and herbicide application did not increase cattle performance overall. Moreover, we did not find a significant relationship between *L. cuneata* abundance and per head yearling cattle weight gain. Our results add to a growing line of evidence that invasive species management does not always increase cattle performance. The hypothesized negative relationship between invasive species abundance and cattle performance may be minimal (or neutral) across large grassland landscapes, particularly those managed with pyric herbivory. To date, pyric herbivory is the only management regime known to simultaneously promote biodiversity, and restrict some invasive plant species like *L. cuneata*. If managers are to meet multiple objectives and buffer against future uncertainty, we must move toward heterogeneity-based strategies for grassland management.

Keywords: Growing season fire, heterogeneity, livestock performance, pyric herbivory, rangeland management, tallgrass prairie

Introduction

Maintaining biodiversity and livestock performance is a persistent dilemma facing many rangeland managers and producers. Moreover, achieving production and biodiversity management goals is further complicated by possible invasive species effects. Competition between undesirable invasive plants and important forage species are broadly thought to result in decreased livestock performance (Cummings et al., 2007; Juliá et al., 2007). Moreover, results from many small-scale studies (i.e., 10 m^2 or less) have suggested that invasion may lead to severe implications for biodiversity and ecosystem function through the homogenization of grassland plant communities (Kennedy et al., 2002; Seabloom et al., 2003; Tilman et al., 2006), while the large-scale effects of invasive plants on ecosystems are mixed at best (Kettenring and Adams, 2011; Peng et al., 2019; Tomasetto et al., 2019). The dominant management strategy to limit invasive species effects is to treat rangelands with broad-scale aerial herbicide applications (Crone et al., 2009; Fuhlendorf et al., 2009b, 2002). Invasive species mitigation with herbicides (whether broad aerial spraying or targeted small-scale applications), however, may have important unintended negative effects on biodiversity and ecosystem function (e.g., collateral damage to non-target native plant and arthropod communities; Crone et al., 2009; Fuhlendorf et al., 2002; Rinella et al., 2009; Sheley et al., 2011), leading to a paradoxical relationship between managing invasive species and maintaining biodiversity across working landscapes.

Pyric herbivory – i.e., the recoupling of fire and grazing to create a mosaic landscape (Fuhlendorf and Engle, 2001) – is well documented as being more effective at limiting the spread of some invasive species than traditional management regimes (Cummings et al., 2007; Sherrill et al., 2022), and may help managers achieve biodiversity (Fuhlendorf et al., 2009a) and livestock production goals (Allred et al., 2014). The interaction between fire and grazing is thought to alter foraging patterns such that typically unpalatable invasive species are kept at more palatable stages of growth (i.e., reduces grazer selectivity), resulting in disturbances that may restrict some invasive species (Cummings et al., 2007). Some have suggested that the use of fire or herbicide alone may be ineffective for many well established invasive species, and that studies should investigate whether an integrated approach (e.g., the interactive effect of fire and herbicide) might be more effective (Cummings et al., 2007; DiTomaso et al., 2006). Integrated management strategies with fire and herbicide treatment are already being applied across many rangelands in the Great Plains, but few studies have addressed whether these approaches are benefiting livestock producers in the region.

Studies across the Great Plains generally have not measured how fire timing (i.e., what season fire is applied), herbicide application, or invasive species abundances affect livestock performance although effects on plant communities are broadly studied (Boughton et al., 2013; Brockway et al., 2002; Dickson et al., 2019; Meyer and Schiffman, 1999; Vermeire et al., 2011). Rather, what effect invasive species management – and the invasive species itself – has on cattle performance is largely assumed based on forage responses alone (Sheley et al., 2011). Moreover, much of the fire-grazing-herbicide literature (and subsequent management) is based on studies conducted at single or small scales (e.g., 1m^2 plots) that cannot capture (or are designed to eliminate) the full range of complexity typical of rangeland landscapes, are poorly replicated, or fail to test management strategies that are relevant to managers and livestock producers (e.g., fail to include grazers in experimental design, herbicide or fire applications do not represent current management, etc.; Alexander et al., 2021; Dickson et al., 2019; Duncan et al., 2021; Towne and Craine, 2016).

In the Flint Hills of North America the dominant management strategy to both optimize desirable forage biomass and reduce invasive species (or other noxious weeds) is to conduct large-scale burns (i.e., whole pasture or ranch-wide) in the early spring (usually April; Towne and Craine, 2016), and aerially apply herbicides that target broadleaf forbs across whole pastures (e.g., 2,4-D, [(2,4-dichlorophenoxy)acetic acid]; Fuhlendorf et al., 2002). Previous research supports that early spring fires promote desirable forage species in the Flint Hills and tallgrass prairie (Anderson et al., 1970; Dickson et al., 2019; Owensby and Anderson, 1967; Towne and Owensby, 1984). Some have suggested that producers shift to burning during the late growing season to better manage some invasive species like *Lespedeza cuneata* (Dum. Cours.) G. Don, and that such changes in management do not negatively affect forage productivity – thus likely not affecting cattle performance (Alexander et al., 2021). However, other than assumptions based on their effect on forage biomass or plant communities, there is no evidence showing whether cattle performance is affected by fire timing, herbicide, or integrated fire-herbicide treatments aimed at reducing invasive species – particularly across landscapes managed with pyric herbivory. Moreover, although management in the Flint Hills region includes strategies specifically aimed at restricting the spread of *L. cuneata*, there is no evidence linking its invasion to reduced cattle performance.

We conducted a replicated, large-scale (i.e., replicates > 300 ha) experiment to analyze whether *L. cuneata* abundance or management approaches aimed at its reduction (namely, fire timing, herbicide, and the fire-herbicide interaction) affects cattle performance in rangelands with pyric herbivory. We specifically set out to test four hypotheses in this study relevant to current management in the Flint Hills region: (H_1) burning during the growing season does not affect cattle performance compared to dormant season burns, (H_2) pastures aerially sprayed with herbicide to control the invasive *L. cuneata* have higher cattle performance compared to pastures where herbicide is not used, (H_3) pastures that are burned and sprayed with herbicide (i.e., the fire-herbicide interaction) have higher cattle performance than pastures that are burned but not sprayed, and (H_4) cattle performance decreases with increased *L. cuneata* abundance.

Methods

Study Area and Experimental Design

Our study took place at the Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve (hereafter TPP); a 16,000-ha tract of remnant tallgrass prairie in the southern Flint Hills region of the North American Great Plains. The TPP is dominated by tallgrass prairie vegetation (e.g., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Dalea candida* Michx. Ex Willd., *Echinacea pallida* (Nutt.) Nutt., *Liatris* spp., *Asclepias* spp., etc.). Temperature and precipitation are highly variable across the TPP, which is typical for grassland ecosystems globally, but annual averages range from 13 to 16 ℃ and 100 to 200 cm, respectively (Brock et al., 1994; McPherson et al., 2007).

The northern portion of the TPP is subdivided into 8 distinct pastures encompassing more than 4,500 ha total, ranging from 333 – 766 ha each. Each landscape was moderately grazed (0.37 animal units $\cdot$ ha^{-1}) from April to September, 2018-2020. Further, each pasture was divided 3 relatively equal patches, and a different patch was burned per year so that all patches in each pasture were eventually burned after three years. Animals in each pasture had unrestricted access to both burned and unburned patches, following the pyric herbivory paradigm (Fuhlendorf et al., 2009a; Fuhlendorf and Engle, 2004, 2001). Our pastures were stratified such that four of them each had a single patch burned in the dormant season (March – April), and the other four had a single patch burned in the growing season (August – September; Figure 1). Additionally, we aerially applied the herbicide Metsulfuron Methyl (Methyl 2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]-carbonyl]amino]sulfonyl]benzoate) to two randomly selected dormant season and growing season-burned pastures. Herbicide was applied at the end of the growing season across the most recently burned patch in the sprayed pasture (October of each year), following a full growing season of vegetative growth (Figure 1). Our herbicide regime was intended to target *L. cuneata* while limiting negative effects on other broadleaf forbs by spraying later in the growing season (Koger et al., 2002; Sherrill et al., 2022). Moreover, previous field trials have suggested that spraying following a full growing season maximizes herbicide contact with *L. cuneata* leaf surfaces. Patches burned in the growing season were not sprayed with herbicide until the year following the burn (e.g., 2018 growing season burn patch would not be sprayed until October 2019), whereas dormant season burn patches were sprayed the same year that the burn occurred but at the end of one full growing season (Figure 3.1). Therefore, all pastures that were treated with herbicide had comparable growing-season days between when the fire occurred and when they were sprayed.

Data Collection and Analysis

We collected *L. cuneata* canopy cover data across all of our pastures from mid-July to August from 2019-2021 to assess whether cattle performance declined with increased L. cuneata abundance (H_4). We sampled *L. cuneata* across 7 transect arrays established within each burned patch across all 8 of our pastures (21 arrays per pasture; 168 arrays total). Each array consisted of two intersecting 60-m transects arranged to form a cross pattern roughly in all four cardinal directions (Figure 3.2). The location of each array was randomly generated, but were distributed so as to avoid wetlands, roads, and fence-lines by 500m. Beginning at the western end of the array, we sampled *L. cuneata* occurrence and abundance using 0.1m^2 frames every 5 meters across each transect in the array (Daubenmire, 1959; Figure 2). We estimated *L. cuneata* abundance in each 0.1m^2 frame using canopy cover classes on a scale from 1-9 representing a range of cover values (trace, 0-1, 1-2, 2-5, 5-10, 10-25, 25-50, 50-75, 75-95, and 95-99% respectively; McMillan et al., 2019; Peet et al., 1998).

We used cattle weight gain per head to determine cattle performance across each of our pastures. Cattle were weighed immediately, *en masse* by the truckload, before they entered each pasture, and again immediately after they were removed each year of our study. Truckloads of cattle were randomly assigned to each pasture. Cattle were treated the same regardless of their pasture assignment. Each pasture had a sustained stocking rate of 0.37 animal units · ha^{-1}. We calculated the per-head weights for each pasture by dividing the total truckload weights by the total number of cattle upon their arrival in April and after exiting the pasture in September. The weight gained per head from each pasture was the difference between the per head entrance and exit weights, and did not require a correction for potentially lost (i.e., due to death, escape, etc.) individuals from each pasture.

We analyzed the relationships between cattle performance (i.e., weight gain) and fire-timing, herbicide treatment, the fire-herbicide interaction, and *L. cuneata* abundance using a two-way analysis of variance (ANOVA) with an interaction and linear modelling techniques. Our fire-timing and herbicide treatments were applied using a 2-by-2 factorial experimental design, and therefore were analyzed using a two-way ANOVA with an interaction term to investigate the interaction between fire-timing and herbicide (i.e., $H_1 – H_3$). To test whether *L. cuneata* abundance correlated with cattle weight gains (H_4), we first converted our cover values to a midpoint percentage value (e.g. a 0.1m^2 frame with 5-10% cover of *L. cuneata* would be considered as having 7.5% cover in our analysis). We then performed a linear regression using the data in the program R version 4.1.2 (R Core Team, 2021), with the mean *L. cuneata* cover and the corresponding average weight gained per head across each pasture as the independent and dependent variables, respectively. We declared significance at $\alpha = 0.05$ for all statistical tests.

Results

From 2018 – 2020, we weighed 5,950 total cattle, averaging 1,983 cattle per year to determine whether fire-timing, herbicide, or their interaction significantly affected cattle weight gain ($H_1 – H_3$). Cattle across all eight of our pastures gained approximately 149.05 $\text{kg}\cdot\text{head}^{-1}\cdot\text{year}^{-2}$ on average (SE = 4.03). We rejected our hypothesis (H_1) that cattle weight gain was not affected by fire-timing, and found that cattle productivity was significantly lower in pastures burned during the growing season ($\bar{x} = 134.60$ $\text{kg}\cdot\text{head}^{-1}$, SE = 3.84) compared to those burned during the dormant season ($\bar{x} = 158.10$ $\text{kg}\cdot\text{head}^{-1}$, SE = 5.79) (F = 19.17, $p < 0.01$, df = 1,25; Figure 3.3). We also rejected our hypotheses that herbicide treatment (F = 1.68, p = 0.20, df = 1,25; Table 3.1; H_2) and the interaction between fire-timing and herbicide (F = 0.26, p = 0.61, df = 1,25; Table 3.1; H_3) increases cattle weight gain, and found no significant effect on cattle productivity of either treatment across our pastures.

We sampled 8,064 plots overall to assess whether *L. cuneata* abundance is negatively related to cattle weight gain (H_4). Average *L. cuneata* cover was 6.20% (SE= 0.80) across all of our pastures from 2019 to 2021. Furthermore, average *L. cuneata* cover for each pasture ranged from 0.49 – 14.56%. We rejected our hypothesis that *L. cuneata* cover reduces cattle weight gain (H_4). We instead found that increased cover did not significantly affect cattle weight gains observed across our study area from 2019 to 2021 (linear regression; p = 0.82, Figure 3.4).

Discussion

Growing season fires, herbicide application, or employing integrated management (i.e., the interaction between fire and herbicide) approaches to manage *L. cuneata* did not increase cattle performance compared to pastures that received dormant season fire-only treatments. Our results also suggest that there is no relationship between *L. cuneata* abundance and cattle performance on rangelands where the average cover across the whole landscape is 15% or less. An integrated management approach (i.e., applying both fire and herbicide) is often promoted as a way to successfully combat the negative effects of well-established invaders, including *L. cuneata* (Cummings et al., 2007). We show that integrating herbicide into fire management regimes – particularly pyric herbivory – may not increase livestock performance across rangelands invaded by *L. cuneata*. *L. cuneata* is assumed to reduce the production potential of invaded rangelands by displacing other more palatable forages. However, previous research shows that *L. cuneata* may not negatively affect forages at large scales (Cummings et al., 2007; Sherrill et al., 2022). Moreover, *L. cuneata* remains highly palatable and nutritious for cattle during early growth after a prescribed fire, and is heavily grazed during those times (Cummings et al., 2007; Sherrill et al., 2022), thereby supporting a possible neutral effect on cattle weight gains in rangelands with pyric herbivory. Dormant season fires favor highly palatable bunchgrasses in the tallgrass prairie (Dickson et al., 2019; Engle and Bidwell, 2001; Owensby and Anderson, 1967; Towne and Owensby, 1984), and have long been known to have a significant influence on cattle weight gains in the region (Anderson et al., 1970). Therefore, if rangeland managers intend to optimize cattle performance across rangelands invaded by *L. cuneata*, choosing when to burn may be more important than invasive species mitigation (e.g., choosing what chemical to spray), especially if those rangelands are managed with pyric herbivory.

It is well-known that fire significantly influences livestock performance in the tallgrass prairie, however when and how to best integrate fire into livestock management remains debated across the region. Dormant season prescribed fires, particularly those in the late spring (March-April), have historically been used to optimize cattle productivity across the Flint Hills region of Kansas and Oklahoma (Anderson et al., 1970; Towne and Owensby, 1984). However, there are notable negative tradeoffs associated with dormant season fires, including for biodiversity conservation (Boyd and Bidwell, 2001). Some have specifically recommended that rangeland managers in the region switch to burning during the growing season to restrict *L. cuneata* invasion, and suggest that there are no negative consequences of that regime on cattle performance (Alexander et al., 2021; Duncan et al., 2021). However, we show that even when managing rangelands with pyric herbivory – a process critical to biodiversity (Fuhlendorf et al., 2009a; Fuhlendorf and Engle, 2001; Hovick et al., 2015; McGranahan et al., 2018) and that might suppress invasion (Cummings et al., 2007; Sherrill et al., 2022) – restricting fire-timing to the growing season significantly reduced stocker performance compared to landscapes burned during the dormant season. Others have found that crude protein (i.e., % Nitrogen) levels of forage were lower in growing season-burned patches the following spring than levels found in forages from the current year's dormant season burn patches. Crude protein levels from forages in patches burned during the growing season did not equal or exceed those from dormant season burned patches until after the current years' growing season burn was performed, providing 60 days less of high quality forage from growing season burns than dormant season prescribed fires (Allred et al., 2011a). If our cattle experienced similar forage quality, our stockers that grazed pastures during the growing season could have had lower quality forage for a third of their grazing period when compared to those grazing dormant season burned patches. To date, pyric herbivory (Fuhlendorf and Engle, 2001) is the only management regime known to simultaneously help producers meet biodiversity and livestock performance goals, as well as restrict invasive species like *L. cuneata* (Cummings et al., 2007; Sherrill et al., 2022). We suggest that future research continue to unravel cattle performance response to fire timing across landscapes managed with pyric herbivory.

Invasive species do not always reduce livestock performance, and therefore their management may not always be warranted or necessary, especially across large heterogeneous grasslands. Invasive species are assumed to reduce livestock performance because they competitively exclude and reduce the abundance of important forages (Sheley et al., 2011). However, the research supporting the exclusionary relationship between invasive species and other plants are primarily limited to small-scale studies (Fuhlendorf et al., 2009b; Kettenring and Adams, 2011), designed to eliminate (or control) the variance that is characteristic of large grasslands. It has been heavily debated for at least three decades whether invasive species effects on ecosystems are always negative, or whether their effects are neutral (or positive) across large scales (Fridley et al., 2007; Kettenring and Adams, 2011; Peng et al., 2019; Tomasetto et al., 2019). For instance, it is likely that invasive species effects become positive at large spatial scales because they are both limited by, and contribute positively to, landscape heterogeneity that increases with scale (Davies et al., 2005). Increased landscape heterogeneity has been tied to increased rangeland biodiversity (Hovick et al., 2015) and resiliency for producers (Allred et al., 2014). Conversely, invasive species mitigation efforts like herbicide application are known to have unintended negative effects on biodiversity and ecosystem function (Fuhlendorf et al., 2002; Rinella et al., 2009), and may reduce landscape heterogeneity (Fuhlendorf et al., 2009b). Results from small scale invasive species research are, by design, unlikely to translate to large working rangelands, and cannot adequately capture the effects of invasion or mitigation efforts on landscape function. Therefore, managers and livestock producers should be cautious when applying results from small scale studies to heterogeneous grasslands, and carefully consider whether pursuing invasive species mitigation is worthwhile given their objectives.

Conclusion

Strategies to reduce *L. cuneata* invasion like prescribed burning during the growing season, herbicide treatment, or integrated management with fire and herbicide did not increase cattle performance in our study. Moreover, *L. cuneata* invasion may not affect cattle performance, especially when average landscape canopy cover is less than 15%. Rather, cattle performance was more affected by fire-timing alone, with cattle gaining more weight in pastures burned during the dormant season than those burned during the growing season. Herbicide treatment is fraught with issues (Fuhlendorf et al., 2009b), and our research supports that applications aimed at reducing invasive species may not accomplish livestock performance objectives. Pyric herbivory and dormant season fires may be sufficient to limit *L. cuneata* invasion without sacrificing livestock performance. However, restricting fire-timing to the dormant season may also lead to unintended negative effects on biodiversity (Boyd and Bidwell, 2001; Reinking, 2005) and society (Towne and Craine, 2016). Managers should consider integrating variable fire timing (i.e. alternating between dormant and growing season fires; Fuhlendorf and Engle, 2001) into the pyric herbivory management framework to balance the tradeoffs of only burning during either the dormant or growing season in isolation. It is unlikely that invasive species always have a negative effect on cattle performance, and the relationship between many species and livestock remains unknown across large complex rangelands. If producers are seeking to maintain livestock performance and biodiversity across invaded rangelands, they should shift their attention toward heterogeneity-based management approaches known to achieve those objectives.

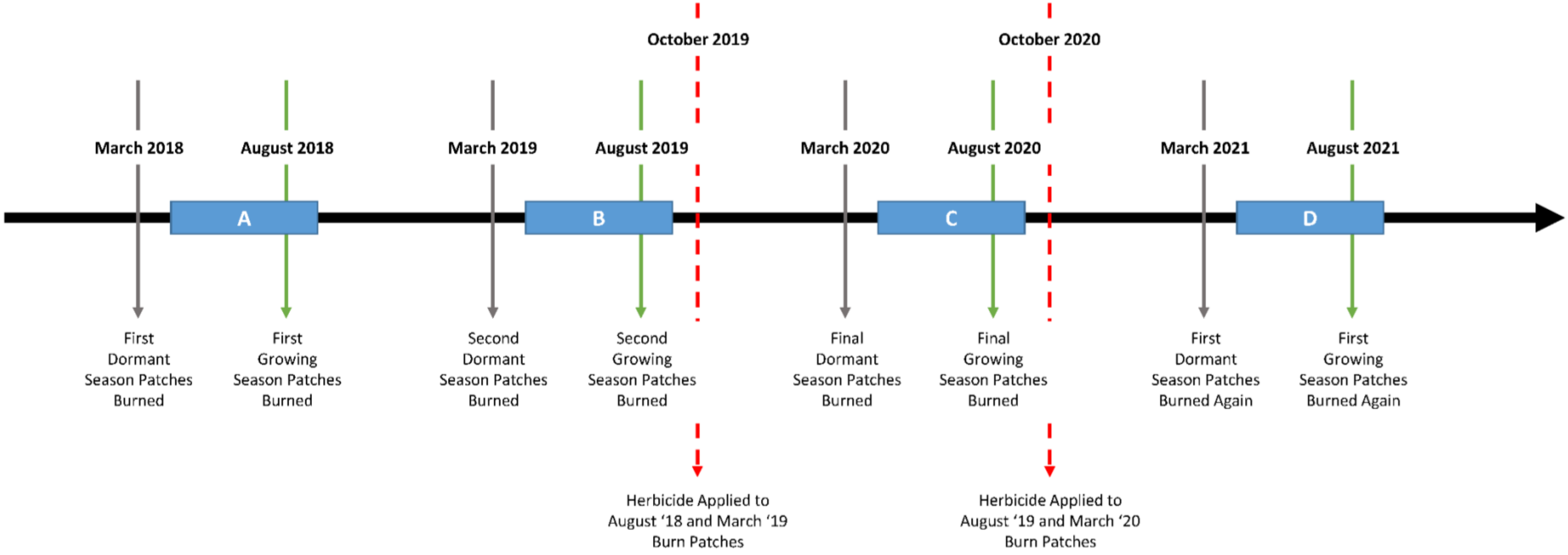

Figure 3.1: Timeline showing when fire and herbicide treatments occurred, as well as the burn-date for patches that received an herbicide application, across all of our pastures. Timeline also shows when cattle were present in our pastures (i.e., April – September) during the four years of our study (i.e., A-D).

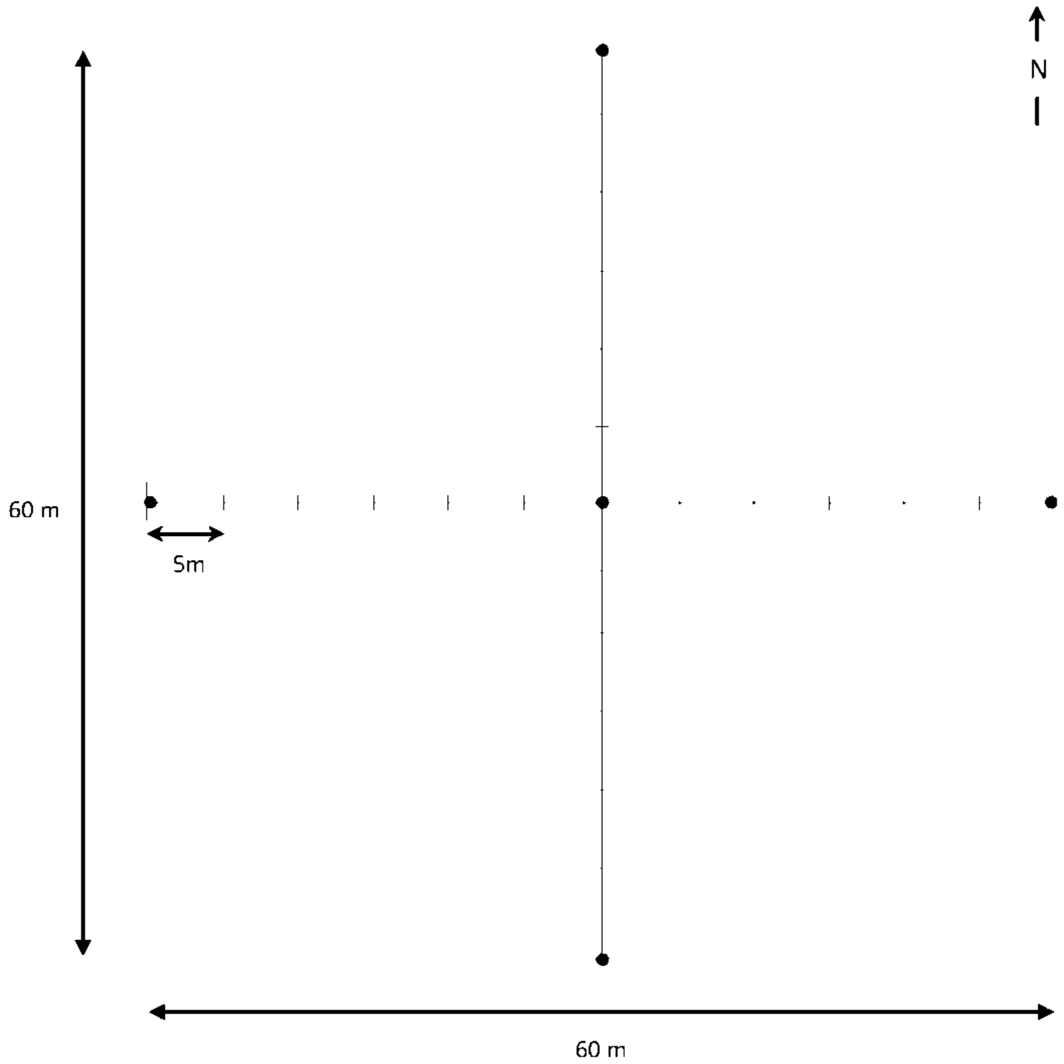

Figure 3.2: The layout of a single transect array. Each tick-mark represents the location of a single 50 x 20 cm plot (0.1 m^2). Transects were all oriented following the four cardinal directions (North, South, East, West).

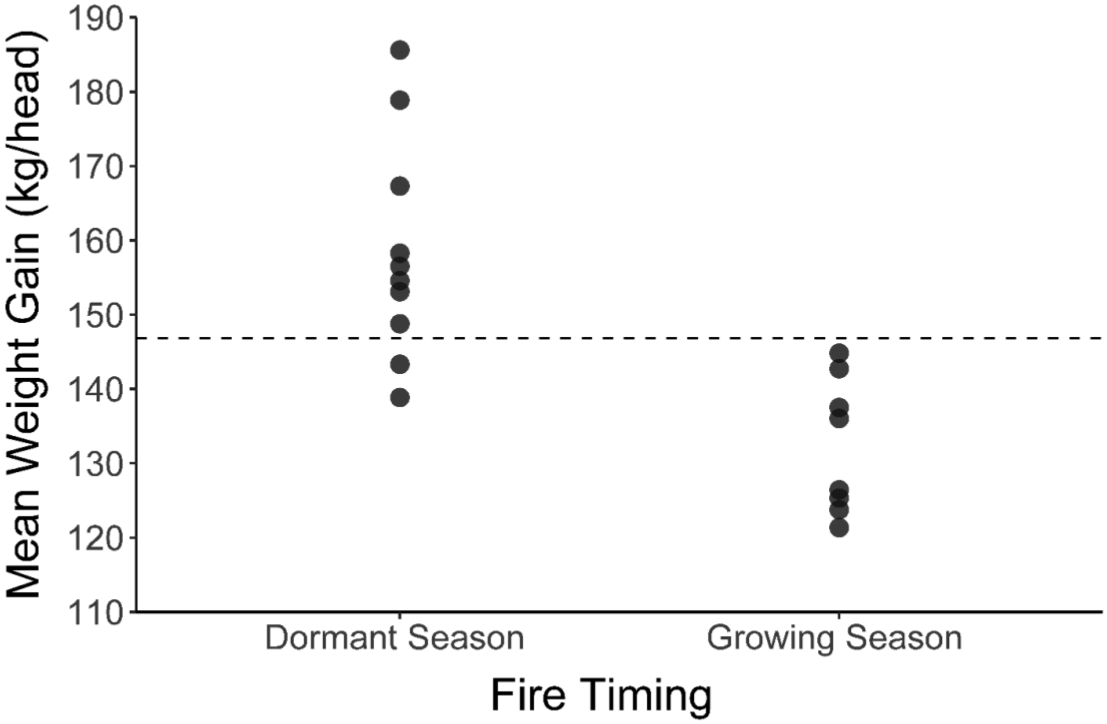

Figure 3.3: Mean cattle weight gain (kg/head) across our study pastures that were burned in the spring or summer. Spring fires occurred between March and April, and summer fires between August and September. Points represent mean weight gained for each pasture per year within each treatment. Data represents conditions from 2018 – 2020. Dashed line represents the overall mean of our weight gain data. Data only represents pastures that were not sprayed with herbicide. Note: there is unequal sampling between our two treatments, as one pasture in the growing season treatment was split into two following the 2019 grazing season. Our two-way ANOVA was still robust despite unequal sampling. 264 cattle were weighed per pasture on average for the duration of our study, and pasture averages ranged from 132 to 376. Cattle numbers in each pasture were set to maintain a moderate stocking rate (0.37 animal units · ha^{-1}) every year.

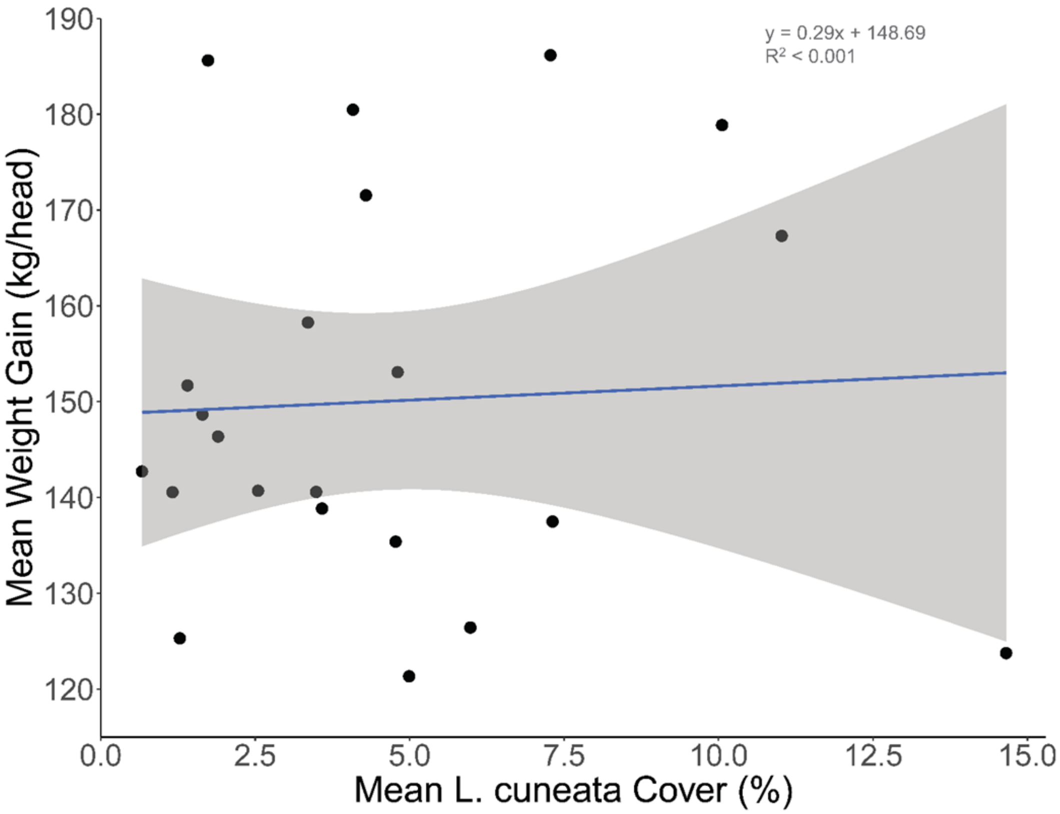

Figure 3.4: Mean cattle weight gain (kg/head) in each pasture relative to the corresponding mean recorded Lespedeza cuneata (i.e., sericea lespedeza) canopy cover (%). Mean L. cuneata cover was not a significant predictor of weight gained across our pastures (regression; $p = 0.82$, df = 20, Adj. R-squared < 0.001; $\alpha = 0.05$), irrespective of treatment (i.e., burn season or herbicide). Shaded area represents a 95% confidence interval around the mean. Line included to show directionality, not to indicate significance.

CHAPTER IV

A PLEA FOR SCALE, AND WHY IT MATTERS FOR INVASIVE SPECIES MANAGEMENT, BIODIVERSITY, AND CONSERVATION

Abstract

Invasive species are suspected to be major contributors to biodiversity declines worldwide. However, invasive species effects are likely scale-dependent, and are hypothesized to paradoxically be positively related to biodiversity at large spatial scales. Moreover, management against invasion can negatively or positively affect biodiversity. Some have suggested that altering disturbance timing (e.g., fire-timing), or integrating herbicide into other land management practices may be sufficient to restrict some invasive species without negatively affecting biodiversity. However, replicated experimental evidence supporting many of these actions is lacking across large landscapes, particularly those managed with pyric herbivory (i.e., the recoupling of fire and grazing). We manipulated eight large (333 – 809 ha) experimental landscapes with pyric herbivory to test how an invasive legume (i.e., *Lespedeza cuneata*), and management aimed at its reduction (i.e., growing season fire and herbicide), affects grassland plant communities at scales ranging from 0.1 m^2 to >3,000,000 m^2. After three years of differing fire and herbicide regimes, our treatments did not differ in their long-term (>1 year) ability to reduce *L. cuneata* abundance. The effect of our treatments on biodiversity were not uniform across scales or diversity metrics, but did not result in widespread collateral damage. The effects of *L. cuneata* invasion on grassland plant communities changed with scale; being negative at small scales (0.1 m^2) and neutral or positive at large scales (>3,000,000 m^2). Invasive species effects gleaned from small scale studies do not reliably predict their effects at larger scales. Therefore, management strategies based on results from small-scale studies of invasion are unlikely to increase or conserve biodiversity across large scales. Rather, processes that generate landscape heterogeneity are probably more important to promoting biodiversity across all scales. Scale is the central problem in ecology, and defining scale in management objectives is essential to effective biodiversity conservation.

Keywords: Fire-timing, Herbicide, Heterogeneity, *Lespedeza cuneata*

Introduction

Invasive species are touted as significant contributors to the global biodiversity crisis (Didham et al., 2005; Doherty et al., 2016), and are central players in what some have dubbed the Homogocene Epoch (Rosenzweig, 2001). In general, high biodiversity is frequently a desired characteristic across conservation areas, and is hypothesized to confer increased functional redundancy and resiliency compared to ecosystems with low biodiversity (Tilman et al., 2006). Invasion by non-native species has been linked to negative effects on biodiversity, eventually leading to system degradation (Doherty et al., 2016). As such considerable energy is put into invasive species reduction worldwide to mitigate biodiversity and ecosystem function losses (e.g., homogenization) due to invasion (Kopf et al., 2017).

Data supporting negative effects of invasive species on biodiversity are mostly limited to highly manipulated, small-scale studies, and evidence for negative relationships between invasive species and biodiversity across large, highly-complex landscapes is rare (Kettenring and Adams, 2011; Peng et al., 2019). Biodiversity losses due to invasion are thought to be driven by inter-species competition for space and resources, where invaders disproportionately outcompete and exclude native species (Fridley et al., 2007; Kettenring and Adams, 2011; Peng et al., 2019). However, the negative invasion-diversity relationship has been shown to paradoxically become neutral -- or possibly even positive – with increasing spatial grain or extent (Fridley et al., 2007; Peng et al., 2019; Stohlgren et al., 2006, 2003, 1999; Tomasetto et al., 2019). Some have argued that the invasion paradox is the result of accumulated landscape heterogeneity, where the extent of invasion is limited by biotic and abiotic forces at large scales, and interspecies competition at small scales (Davies et al., 2005; Kumar et al., 2006). As invasive species become more spatially limited with increasing scale, their presence adds to the total species pool across the landscape (i.e., more species are able to coexist), leading to a positive diversity-invasion relationship (Davies et al., 2005). Undoubtedly small-scale experimental studies (i.e., $\leq 10m^2$) are incapable of capturing – or are designed to eliminate – the full range of heterogeneity that likely drives species diversity dynamics across large landscapes (Fuhlendorf et al., 2017). Relatively recent meta-analyses have revealed that even at small spatial scales, the invasion-biodiversity relationship is highly variable, depending on the study system, experimental design, and even the authors involved (Tomasetto et al., 2019). Importantly, the invasion paradox highlights that results from heavily manipulated, homogenous, small-scale studies are likely not transferrable to heterogeneous, real-world landscapes. Management efforts worldwide generally do not reflect the data from investigations of the invasion paradox, however. Instead, management is often focused on invasive species reduction – even at great financial cost (Kopf et al., 2017) – to thwart a biodiversity crisis driven by invasion (Didham et al., 2005; Doherty et al., 2016).

Rationales for grassland management actions targeting invasive species reduction include, generally, to increase biodiversity and buffer against livestock productivity losses – i.e., from the exclusion and reduction of palatable forage species by less palatable or toxic invaders (e.g., *Bromus tectorum* or *Centaurea stoebe*; cheatgrass or spotted knapweed, respectively). However, some of the more popular methods commonly employed to reduce invasive species (e.g., herbicide application) also carry negative consequences for biodiversity (Crone et al., 2009; Fuhlendorf et al., 2002; Rinella et al., 2009; Stokely et al., 2021). Moreover, disturbance processes (e.g., fire and grazing) that are critical to biodiversity maintenance in many systems also favor invasion (Hobbs and Huenneke, 1992; Lear et al., 2020). For example, in the Great Basin of North America, cheatgrass (*Bromus tectorum* L.) invasion has been linked to altered fire frequencies and phenological shifts in forages that threaten native biodiversity (Germino et al., 2016) and livestock production (Currie et al., 1987; Morrow and Stahlman, 1984) across the region. Frequent fire and grazing disturbances also favor increased spread for cheatgrass (Germino et al., 2016), suggesting a positive feedback between disturbance and invasion for that species.

Therefore managers face a dilemma – how to simultaneously manage grasslands using processes that promote biodiversity, while limiting or reducing invasive species abundance.

In the Flint Hills of North America the invasive species *Lespedeza cuneata* (Dum. Cours.) can be successfully managed using pyric herbivory (i.e., the recoupling of fire and grazing disturbances; (Cummings et al., 2007; Fuhlendorf and Engle, 2001; Sherrill et al., 2022). Pyric herbivory is a process that promotes landscape heterogeneity critical to grassland biodiversity maintenance (Fuhlendorf et al., 2009a). Some suggest that integrating herbicide into pyric herbivory management regimes (Cummings et al., 2007) or burning during the growing season (Alexander et al., 2021) might be more effective at reducing *L. cuneata* invasion without negative biodiversity implications. While there is some evidence that fire-timing may have a significant influence on grassland plant community composition (Dickson et al., 2019), the synergistic effect of fire-timing and grazing is omitted from the extant grassland plant ecology literature overall – i.e., including their effects on invasive plants. Moreover, replicated experimental evidence showing that growing season fires reduce *L. cuneata* abundance compared to those in the dormant season is lacking, particularly from grasslands managed with pyric herbivory. Although invasive species are broadly managed in rangeland systems to prevent forage productivity losses (Cummings et al., 2007; Juliá et al., 2007), data supporting that *L. cuneata* reduces important plant functional groups (i.e., grasses, sedges, forbs, etc.) are mixed at small or intermediate scales (Cummings et al., 2007; Sherrill et al., 2022), and remain largely unknown across large spatial scales. Therefore, critical information regarding how to manage large grasslands for biodiversity conservation, and what broad effects that invasive species have across those landscapes, is lacking.

We analyzed a robust vegetation community dataset from 8 experimental landscapes managed with pyric herbivory to investigate the relationships between scale, invasion, management, and biodiversity. We specifically set out to test the following hypotheses at scales ranging from the plot (i.e., $0.1m^2$) to the landscape (i.e., $>10^6$ m^2), with *L. cuneata* as our targeted invader: (H_1) *L. cuneata* abundance is more negatively affected by fires during the growing season than during the dormant season; (H_2) integrating herbicide into pyric herbivory management regimes more effectively reduces *L. cuneata* abundance than management with pyric herbivory alone; (H_3) landscapes burned during the growing season or (H_4) that use integrated management with pyric herbivory and herbicide have higher plant diversity compared to landscapes managed without those efforts (i.e., pyric herbivory with dormant season fire); (H_5) *L. cuneata* abundance is negatively related to biodiversity; and (H_6) *L. cuneata* abundance is negatively related to other plant functional group abundances.

Materials and Methods

Study Area and Experimental Design

Our study took place at the Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve (hereafter TPP); a 16,000-ha tract of remnant tallgrass prairie in the southern Flint Hills region of the North American Great Plains (Appendix A). The TPP is dominated by tallgrass prairie vegetation (e.g. *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Dalea candida* Michx. Ex Willd., *Echinacea pallida* (Nutt.) Nutt., *Liatris* spp., *Asclepias* spp., etc.). Temperature and precipitation are highly variable across the TPP, which is typical for grassland ecosystems globally, but averages range from 13 to 16 ℃ and 100 to 200 cm annually (Brock et al., 1994; McPherson et al., 2007).

The northern portion of the TPP is subdivided into 8 distinct experimental landscapes encompassing more than 4,500 ha total, ranging from 333 – 766 ha each. Each landscape was moderately grazed (0.37 animal units $\cdot$ ha^{-1}), April to September, from 2018-2020 (Appendix A). Further, each experimental landscape was divided into thirds (patches), where a different third of each landscape (i.e., a different *patch*; Appendix A) was burned per year, following the patch-burn paradigm (Fuhlendorf et al., 2009a; Fuhlendorf and Engle, 2004, 2001). Patches were burned so that they each had a three-year fire return interval (i.e., would not be burned but once every three years). Our experimental landscapes were stratified such that four of them each had a single patch burned in the dormant season (March – April), and the other four with a patch that was burned in the growing season (August – September; Appendix A) every year of the study. We further divided our experimental landscapes such that, within each fire timing treatment (i.e. dormant or growing season), two landscapes received herbicide treatments and two did not (Appendix A). Methyl 2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]-carbonyl]amino]sulfonyl]benzoate (i.e., Metsulfuron Methyl) was aerially applied at the end of the growing season across the most recently burned patch of each experimental landscape in the herbicide treatment (October of each year), after the patch had a full growing season of vegetative growth. We used a light (58.5 $ml \cdot ha^{-1}$) concentration herbicide, applied at a rate of 28 $L \cdot ha^{-1}$ across our treatment areas. We applied herbicide later in the growing season and at low concentrations to target *L. cuneata* and limit the negative influence on other broadleaf forbs – particularly since *L. cuneata* remains in an active vegetative state later in the year than other species (Sherrill et al., 2022). Moreover, spraying following a year of growth maximized the chances that the herbicide would come into contact with *L. cuneata* leaf surfaces, increasing the likelihood of effectiveness. Thus, patches burned in the summer were not sprayed with herbicide until the year following the burn (e.g. summer 2018 burn patch would not be sprayed until October 2019), whereas spring-burned patches were sprayed the same year as the burn occurred. However, our spraying regime also ensured that the two fire-timing treatments had comparable growing season days between the burn and herbicide application.

Data Collection and Analysis

Vegetation data were collected across all of our experimental landscapes annually from mid-July to August 2019-2021. We established 7 vegetation sampling arrays across each burned patch in our experimental landscapes (21 per experimental landscape; Appendices A & B). Each array consisted of two intersecting 60-m transects arranged to form a cross pattern roughly in all four cardinal directions (Appendix B). The location of each array was randomly generated, but was distributed to prevent sampling near wetlands, roads, and fence-lines by 500m. Beginning at the western end of the array, we sampled total species occurrence and abundance using $0.1m^2$ frames every 5 meters across each transect in the array (Daubenmire, 1959; Appendix B). We estimated canopy cover for each species (i.e., an estimate of abundance) in each $0.1m^2$ frame using cover classes on a scale from 1-9 representing a range of cover values (trace, 0-1, 1-2, 2-5, 5-10, 10-25, 25-50, 50-75, 75-95, and >95% respectively; McMillan et al., 2019; Peet et al., 1998). Since our data collection was hierarchically structured across our experimental landscapes (i.e., plots within each array; arrays within each patch; patches within each experimental landscape; Appendices A & B), species abundances at all scales above the plot-level were calculated by averaging the observed canopy cover across all individual observations below the scale of interest. For example, to calculate the average array-scale *L. cuneata* abundance, we summed the *L. cuneata* abundance across all the plots in each array, and divided that value by the total number of plots sampled per array.

We used linear mixed-models to investigate what effect invasive species mitigation strategies (i.e., fire-timing and herbicide application) and *L. cuneata* abundance have on functional group (i.e., grasses and sedges, forbs, and shrubs) abundances, and overall species diversity across our experimental landscapes. Using the "vegan" package in the program R (Oksanen et al., 2016; R Core Team, 2021), we calculated species richness (S), exponential Shannon index (e^H), and inverse Simpson index (D^{-1}) values (i.e., Hill numbers 0, 1, and 2; Chao et al., 2014) to estimate species diversity across our plots, arrays, patches, and experimental landscapes. We paired calculated diversity metrics at each scale with corresponding *L. cuneata* abundance and management data prior to analysis. We utilized linear mixed-models to account for repeated-sampling at each scale, and all models were fit using the "lmerTest" package in R (Kuznetsova et al., 2017; R Core Team, 2021). We also calculated the marginal R^2 for each model – i.e., the variance explained by the fixed-effects of a linear mixed-effects model. For models addressing *L. cuneata* abundance, diversity, or functional group abundances at the experimental landscape scale we used a unique landscape ID as the random intercept term. Models at all other scales used a unique burn patch ID as the random intercept term.

Results

We collected vegetation data from 4,032 individual plots; 168 arrays; 24 burn patches; and 8 experimental landscapes annually from 2019 – 2020. *L. cuneata* canopy cover varied across scales, ranging from 0.0 – 99.0% at the 0.1m^2 plot scale, 0.0 – 59.1% at the array scale, 0.3 – 26.0% at the patch scale, and 0.7 – 14.6% at the experimental landscape scale (Table 4.1). Of the 273 species we documented, approximately 68% (187 spp.) were forbs; 27% were grasses and sedges (74 spp.); and 3% were shrubs (12 spp.).

To evaluate whether growing season fires (H_1) or herbicide application (H_2) reduces *L. cuneata* invasion, we compared abundance data collected from our experimental landscapes burned during the growing season to those burned during the dormant season, and those treated with herbicides against those without. Contrary to our prediction (H_1), *L. cuneata* cover did not differ between patches burned during the dormant or growing season at any scale considered in this study (Figure 4.1). However, we found mixed support for H_2 overall, as the effect of herbicide application on *L. cuneata* varied across scales. Our herbicide treatment was significantly effective at reducing *L. cuneata* at the plot scale for two years post-application, and for one year post-application at the array scale (Figure 4.1). *L. cuneata* abundance increased to pre-treatment levels by the second year post-application at the array scale (Figure 4.1). Our integrated management approach with herbicide did not significantly reduce *L. cuneata* at all other scales considered in this study (Figure 4.1).

To determine whether growing season fires promote higher diversity compared to those during the dormant season (H_3), we compared plant species diversity across landscapes that received either dormant or growing season fire treatments. We found that landscapes burned during the growing season were only marginally higher than those burned during the dormant season at the patch scale, and only for Exponential Shannon diversity (Table 4.2). Otherwise, fire timing did not significantly affect diversity at any other scale or metric we addressed in this study (Table 4.2).

To determine whether integrating herbicide application into pyric herbivory promotes higher diversity compared to those during the dormant season (H_4), we compared plant species diversity across landscapes that were sprayed to those that were not, as well as across a time-since-herbicide gradient. We found mixed support for our hypothesis (H_4), as the effect of herbicide treatment on plant species diversity across our experimental landscapes varied both with scale, and among diversity metrics. Our herbicide treatment had a significant negative effect on species richness across all of the scales we measured, and the negative effect persisted for up to two years post-application (Appendix C). Our herbicide treatment also had a significant negative effect on Exponential Shannon and Inverse Simpson diversity at the plot scale, and the effect persisted up to two years post-application (Appendix C). Our herbicide treatment did not have an effect on Exponential Shannon diversity across all other scales. However, we found that Inverse Simpson Diversity significantly increased at the array scale for one year post-herbicide application. The effect on Inverse Simpson diversity was not significantly different from pre-application levels by two years post-treatment (Appendix C). Our herbicide treatment did not have a discernable effect on Exponential Shannon and Inverse Simpson diversity at the patch and experimental landscape scales.

We analyzed support for our hypothesis that *L. cuneata* abundance is negatively related to plant diversity (H_5) by modeling *L. cuneata* canopy cover against corresponding species richness, Exponential Shannon, and Inverse Simpson diversity indices at scales ranging from the plot to the experimental landscape. We found mixed overall support for our hypothesis (H_5), as the effect that *L. cuneata* had on all of our diversity indices changed with scale, with statistical significance increasing with decreasing scale (Table 4.3, Figure 4.2). We found a negative relationship between *L. cuneata* and both Exponential Shannon and Inverse Simpson diversity indices at the plot (95% CI = [-0.02, -0.03] and [-0.02, -0.03]), array (95% CI = [-0.15, -0.07] and [-0.12, -0.06]), and patch (95% CI = [-0.63, -0.07] and [-0.59, -0.19]) scales. *L. cuneata* canopy cover did not have an effect on Exponential Shannon (95% CI = [-0.52, 0.70]) and Inverse Simpson diversity (95% CI = [-0.61, 0.72]) at the experimental landscape scale (Table 4.2; Figure 4.2). We observed a weakly significant negative effect of *L. cuneata* on Species Richness at the plot (95% CI = [-0.02, -0.01]) and array (95% CI = [-0.21, -0.06]) scales (Table 4.3, Figure 4.3). However, we were unable to detect an effect on Species Richness at the patch (95% CI = [-0.80, 0.11]) and experimental landscape (95% CI = [-0.87, 0.83]) scales (Table 4.3; Figure 4.2). *L. cuneata* did not have a detectable effect on any diversity metric we measured at the experimental landscape scale (Table 4.3; Figure 4.2).

We evaluated whether *L. cuneata* abundance has a negative effect on plant composition (H_6) by modeling *L. cuneata* canopy cover against forb, shrub, and grass and sedge canopy cover measured at scales ranging from the plot to the experimental landscape. *L. cuneata* abundance did not have a uniform effect on any of the functional group abundances we analyzed, and therefore we found mixed support for our hypothesis across scales and functional groups. We found that *L. cuneata* had a significant negative effect on grass and sedge abundances at the plot (95% CI = [-0.24, -0.20]) and array (95% CI = [-0.32, -0.12]) scales. However, contrary to our prediction (H_6) we found that *L. cuneata* had a significant positive effect on grass and sedge abundance at the experimental landscape scale (95% CI = [0.22, 1.45]; Figure 4.3; Appendix D). *L. cuneata* did not have a significant effect on grass and sedge abundances at the patch scale (95% CI = [-0.28, 0.30]). *L. cuneata* had a significant negative effect on forb abundance at the plot scale (95% CI = [-0.14, -0.09]), and a significant positive effect at the experimental landscape scale (95% CI = [0.83, 1.85]; Figure 4.3; Appendix D). *L. cuneata* did not have a significant effect on forb canopy cover at the array (95% CI = [-0.11, 0.08]) or patch (95% CI = [--0.04, 0.48]) scales. *L. cuneata* did not have an effect on shrub abundance at the plot scale (95% CI = [-0.02, 0.01]), but had a significantly positive effect at all other scales. *L. cuneata's* effect on shrub abundance was strongest at the experimental landscape scale (95% CI = [0.15, 0.47]; Figure 4.3; Appendix D).

Discussion

We show that the effects of *L. cuneata*, and management actions aimed at its reduction, on plant diversity and composition are highly variable, and dependent upon the scale (i.e., spatial grain) of observation and the metric used. For example, although the effect of *L. cuneata* abundance (i.e., canopy cover) on plant diversity and composition became more statistically significant (i.e., the *p*-value) with decreasing scale, the amount of the variance explained by the relationship (i.e., the marginal R^2) remained weak across all scales (Figures 4.2 & 4.3). Further, this suggests that the statistically significant relationship that we show at the smallest spatial scale, may be more an effect of sample size than *L. cuneata*. However, we also show that the relationship between *L. cuneata* and other plant functional groups is complex and may be highly scale dependent; with *L. cuneata* possibly adding to landscape heterogeneity at scales larger than the plot (Figure 4.3). In fact, our data agree with those elsewhere showing that *L. cuneata* invasion may not have a negative effect on plant composition at large scales relevant to livestock production, and biodiversity conservation (Sherrill et al., 2022). Therefore we show that *L. cuneata* may not have a uniformly negative effect on plant diversity or composition across grasslands managed with pyric herbivory.

We show that mitigation efforts meant to reduce *L. cuneata* do not always increase – or even affect – diversity across complex grasslands. In fact, chemical-based mitigation efforts often kill important non-target species (Fuhlendorf et al., 2002; Stokely et al., 2021), and can lead to community simplification – both of which are unlikely to be invasive species management objectives. Even our conservation-oriented herbicide treatment had negative consequences for plant diversity at small scales (Appendix C), and were mostly ineffective at long-term (>1 year) invasive species mitigation (Figure 4.1). Herbicide application is well documented as having the potential to cause cascading negative effects on grassland biodiversity (Crone et al., 2009; Fuhlendorf et al., 2002; Sheley et al., 2011), and managers should consider whether the tradeoffs surrounding herbicide are worthwhile prior to application.

Despite claims to the contrary (Alexander et al., 2021; Duncan et al., 2021), we show that burning during the growing season does not reduce *L. cuneata* abundance compared to landscapes burned during the dormant season (Figure 4.1). Our data supports nearly two-decades of data elsewhere in the tallgrass prairie region showing that fire-timing may not have any significant effect on *L. cuneata* (Sherrill et al., 2022), and may not be an effective way to suppress invasion. Growing season fires also have the potential to negatively affect cattle productivity compared to fires applied during the dormant season (Chapter III), further lessening their utility in the tallgrass prairie management. Therefore, it is unlikely that altering fire-timing from the dormant to growing season is a silver-bullet for rangeland managers and conservationists in the region. Rather, our results add to a growing line of evidence that pyric herbivory alone may be sufficient to simultaneously mitigate invasion (Cummings et al., 2007; Sherrill et al., 2022) and promote biodiversity (Fuhlendorf et al., 2009a; Hovick et al., 2015) across those large grassland landscapes.

Our data cannot reliably be used to characterize the effects of *L. cuneata* invasion when the average canopy cover across a large (i.e., > 400 ha) landscape exceeds 15%. It is likely that if we were able to document the full range of possible *L. cuneata* abundances at a large scale (i.e., from 0-99% canopy cover), eventually there would be a negative influence of invasion at that scale. However, other research suggests that *L. cuneata* may not be capable of reaching those levels needed to exhibit predicted negative effects across such large landscapes, with documented abundances peaking at approximately 20% canopy cover after 19 years without any management to reduce invasion (Sherrill et al., 2022). In fact, the total landscape area that an invasive species can successfully occupy – or the realized niche space for an invader – also decreases with increasing scale and accumulated landscape heterogeneity (Davies et al., 2005), adding to the complexity and scale dependence of invasive species effects. Therefore, our findings likely represent current conditions across the tallgrass prairie, and are relevant to describing the effects of *L. cuneata* invasion at scales important to conservation and management efforts ongoing across the region.

The invasive species management paradigm assumes that with little or no action to suppress invasion, species have the potential to simplify global biodiversity, degrade overall economic activity, threaten human health, and lead us into what has been dubbed the Homogocene (Didham et al., 2005; Rosenzweig, 2001; Schmitz and Simberloff, 1997; Vitousek et al., 1996). Most of the literature supporting negative invasive species effects are limited to small-scale studies (i.e., ≤ 10 m^2; Kettenring and Adams, 2011; Peng et al., 2019), and many suggest that mechanisms operating at equally small scales (e.g., competitive exclusion) may drive those effects (Didham et al., 2005; Fridley et al., 2007). However, species distributions or assemblages across large spatial scales ($>$ 1,000,000 m^2) are not only driven by species interactions (i.e., community structure determined by non-interactive forces), and are more likely the result of species responses to myriad processes that occur at comparable scales (e.g., rainfall patterns, soil characteristics, disturbance regime shifts; Davies et al., 2005; Fridley et al., 2007). Landscape variability increases with scale, therefore the likelihood that invasive species are spatially limited across a landscape also increases with scale (Chesson, 2000; Davies et al., 2005; Shea and Chesson, 2002) – i.e., the likelihood that they can form a stable monoculture across an area decreases. As scale increases and invaders become spatially limited or their distribution shifts through time, they contribute more positively to the mix of species occurring across a landscape, eventually leading to a net increase to diversity at some scale (Davies et al., 2005; Fridley et al., 2007).

Scale is a central problem in ecology (Levin, 1992), and defining scale in management objectives is essential to effective biodiversity conservation. We show that managing large, complex landscapes based on hypothesized invasive species effects from heavily experimental, small-scale studies (i.e., $\leq 10\ m^2$) does little to promote large-scale biodiversity. Moreover, invasive species effects on broader plant functional groups (e.g., grasses and sedges) may be minimal – or non-existent – across large heterogeneous grasslands. It is well established that interspecies interactions change with scale (Wiens, 1989), and it is therefore unlikely that invasive species mitigation efforts across large landscapes alone will result in commonly desired outcomes (e.g., increased landscape biodiversity, more forage for livestock or wildlife), which might be more affected by larger-scale processes (e.g., fire or drought; Fuhlendorf et al., 2009b). The aforementioned is supported by some suggesting that invasive species may be more of a *passenger* of ecological changes rather than the sole *driver* (Didham et al., 2005; MacDougall and Turkington, 2005). Specifically, the passenger-model suggests that invasive species dominance is a product of their ability to exploit larger-scale environmental processes (e.g., disturbance, climate change) more effectively than other – often native – species, rather than being driven by competitive exclusion alone (i.e., the driver-model; MacDougall and Turkington, 2005). The passenger-model of invasion also predicts that reduction (or even eradication) of invasive species may not have a strong impact on ecosystem dynamics, because competitive exclusion is not driving species distribution, composition, and abundance across that system (MacDougall and Turkington, 2005; Myers et al., 2000; Zavaleta et al., 2001). Invasive species mitigation aimed at protecting small, isolated, imperiled habitats (e.g., Santa Barbara Island off the coast of California, poor fens and grassy balds in the southern Appalachian mountains, and sand ridges in south central Florida) or highly restricted species (e.g., ‘I‘iwi on Hawai‘i, or Shortia galacifolia in

South Carolina) may be more justified, however, because their conservation can be more sensitive to some invasive species effects (e.g., allelopathy, nutrient cycle disruptions, altered disturbance patterns). It is imperative, then, that managers explicitly state the scale of concern in their invasive species mitigation objectives (e.g., to increase biodiversity across the Tallgrass Prairie Preserve; to conserve existing *Gratiola amphiantha* at 40-Acre Rock State Heritage Preserve). Without explicitly stating the scale of concern, invasive species mitigation objectives may be obscure, and success often incalculable because managers are unable to accurately track the efficacy of prescribed management actions at that – often large – scale. Without measurable invasive species mitigation objectives, efforts may be unjustified, intangible, and more characteristic of vendetta rather than data-based management.

Conclusion

Invasive species effects are highly scale dependent, and management aimed solely at reducing invasion may not single-handedly contribute to large-scale biodiversity conservation. Rather, processes that generate landscape heterogeneity are likely more important to conserving biodiversity across all scales. Processes that generate landscape heterogeneity (e.g., pyric herbivory) also lead to concomitant increases in biodiversity (Hovick et al., 2015) and ecosystem resiliency (i.e., the amount of destabilizing force that an ecosystem can absorb before it undergoes a state change; Holling and Meffe, 1996). We show that invasive species effects gleaned from small scale studies do not accurately predict their effects at larger scales (Figures 4.2 and 4.3), particularly across large and complex landscapes. Investigating how landscape patterns and processes change with scale is fundamental to understanding and managing rangeland landscapes (Fuhlendorf and Smeins, 1996; Sayre, 2017). As we move through the Anthropocene when most landscapes are predicted to become increasingly fragmented, animal movements more restricted, and climate more variable; landscape heterogeneity will be critical to continued biodiversity conservation (Allred et al., 2013; Crone et al., 2019; Thomas, 2010; unpublished data, N.A. McMillan, S.D. Fuhlendorf, B. Luttbeg, L.E. Goodman, C.A. Davis, B.W. Allred, R.G. Hamilton). Moreover, as conserving biodiversity becomes more complex, prioritizing what habitats and which species to conserve will also become increasingly important (Kareiva and Fuller, 2016). Accurately defining the tradeoffs associated with different management actions is totally dependent upon the scale of objectives. Therefore, efforts aimed at conservation in the Anthropocene – worldwide – must weigh the complex influence of scale and landscape heterogeneity on management actions, particularly as they relate to the role of invasion on ecosystem dynamics.

Table 4.1: Table summarizing the average sampling area, *Lespedeza cuneata* canopy cover (%), standard deviation of *L. cuneata* canopy cover (%), species richness (S), inverse Simpson diversity index (D^{-1}), and exponential Shannon diversity index (e^{H}) at the plot, array, patch, and experimental landscape scales. Values represent data collected July 1-30 from 2019-2021.

Scale	**Average Sampling Area Size**	**Mean (± SE) *L. cuneata* canopy cover (%)**	**Std. Dev. *L. cuneata* canopy cover (%)**	**Mean (± SE) Species Richness (S)**	**Mean (± SE) Inv. Simpson Diversity (1/D)**	**Mean (± SE) Exp. Shannon Diversity (e^{H})**
Plot	0.1 m^2	6.7 (± 0.1)	13.3	6.7 (± 0.1)	3.9 (± 0.1)	4.7 (± 0.1)
Array	1,200.0 m^2	6.7 (± 0.4)	8.2	31.3 (± 0.3)	16.0 (± 0.2)	20.9 (± 0.2)
Patch	[a] 1,821,000 m^2	6.2 (± 0.6)	5.5	73.1 (± 1.3)	37.4 (± 1.0)	49.9 (± 1.0)
Exp. Landscape	[b] 5,480,000 m^2	6.2 (± 0.8)	3.6	108.9 (± 2.0)	56.4 (± 2.1)	75.9 (± 1.6)

[a] Patches ranged in size from 911,000 – 3,885,000 m^2

[b] Experimental landscapes ranged in size from 3,335,000– 7,665,000 m^2

Table 4.2: Diversity response to fire timing (i.e., dormant or growing season) at the plot, array, patch, and experimental landscape (next page) scales. Models fit using linear mixed-models. Landscape ID was used as the random intercept term in models at the experimental landscape scale. Burn patch ID was used as the random intercept term for models at all other scales. Models represent data collected each July 1-30 from 2019-2021. All data are from landscapes managed with pyric herbivory.

Scale	**Diversity Metric**	**Fire Timing**	**Estimate**	**SE**	**t-value**	**p-value**	**Marginal R^2**	**Total Obs.**
Plot	Species Richness	Dormant Season (Intercept)	6.34	0.18	34.41	_< 0.01*_	0.01	12,096
		Growing Season	0.35	0.26	1.35	0.19	0.01	
	Exponential Shannon	Dormant Season (Intercept)	4.56	0.12	38.69	_< 0.01*_	<0.01	12,096
		Growing Season	0.22	0.17	1.30	0.21	<0.01	
	Inverse Simpson	Dormant Season (Intercept)	3.81	0.09	41.68	_< 0.01*_	<0.01	12,096
		Growing Season	0.17	0.13	1.36	0.19	<0.01	
Array	Species Richness	Dormant Season (Intercept)	29.19	0.81	35.83	_< 0.01*_	0.02	504
		Growing Season	1.84	1.15	1.60	0.12	0.02	
	Exponential Shannon	Dormant Season (Intercept)	11.45	0.37	30.67	_< 0.01*_	0.01	504
		Growing Season	0.88	0.53	1.67	0.11	0.01	
	Inverse Simpson	Dormant Season (Intercept)	7.51	0.27	27.27	_< 0.01*_	0.01	504
		Growing Season	0.59	0.39	1.53	0.14	0.01	
Patch	Species Richness	Dormant Season (Intercept)	69.39	2.07	33.54	_< 0.01*_	0.07	168
		Growing Season	5.72	2.93	1.96	0.06	0.07	
	Exponential Shannon	Dormant Season (Intercept)	28.73	1.22	23.48	_< 0.01*_	0.09	168
		Growing Season	3.84	1.73	2.22	_0.04*_	0.09	
	Inverse Simpson	Dormant Season (Intercept)	17.34	0.98	17.71	_< 0.01*_	0.08	168
		Growing Season	2.91	1.38	2.10	0.05	0.08	
Experimental Landscape	Species Richness	Dormant Season (Intercept)	104.92	4.02	26.07	_< 0.01*_	0.08	24
		Growing Season	5.83	5.69	1.02	0.34	0.08	
	Exponential Shannon	Dormant Season (Intercept)	46.86	1.82	25.73	_< 0.01*_	0.14	24
		Growing Season	4.95	2.58	1.92	0.07	0.14	
	Inverse Simpson	Dormant Season (Intercept)	27.87	2.15	12.96	_< 0.01*_	0.11	24
		Growing Season	4.85	3.04	1.59	0.16	0.11	

Table 4.3: Diversity response to *Lespedeza cuneata* canopy cover (%) at the plot, array, patch, and experimental landscape scales. Models fit using linear mixed-models. Landscape ID was used as the random intercept term in models at the experimental landscape scale. Burn patch ID was used as the random intercept term for models at all other scales. Models represent data collected each July 1-30 from 2019-2021. All data are from landscapes managed with pyric herbivory.

Scale	**Diversity Metric**	**Intercept**	**Estimate**	**SE**	**t-value**	**p-value**	**Marginal R^2**	**Total Obs.**
Plot	Species Richness	6.64	-0.02	< 0.01	-16.03	*< 0.01**	0.02	12,096
	Exponential Shannon	4.86	-0.03	0.01	-24.77	*< 0.01**	0.05	
	Inverse Simpson	4.09	-0.03	0.01	-24.16	*< 0.01**	0.05	
Array	Species Richness	30.94	-0.16	0.04	-4.28	*< 0.01**	0.03	504
	Exponential Shannon	12.60	-0.11	0.02	-4.97	*< 0.01**	0.06	
	Inverse Simpson	8.36	-0.08	0.02	-5.10	*< 0.01**	0.07	
Patch	Species Richness	74.38	-0.25	0.23	-1.08	0.28	0.03	72
	Exponential Shannon	32.82	-0.28	0.13	-2.13	*0.04**	0.09	
	Inverse Simpson	21.23	-0.35	0.10	-3.52	*< 0.01**	0.17	
Experimental Landscape	Species Richness	107.67	-0.64	0.53	-1.21	0.24	<0.01	24
	Exponential Shannon	48.72	-0.29	0.35	-0.82	0.42	<0.01	
	Inverse Simpson	29.86	-0.35	0.39	-0.90	0.38	<0.01	

Table 4.4: Summary table outlining the six hypotheses (H_1 – H_6) we tested, as well as whether we rejected or failed to reject each across the four scales considered in our study (i.e., experimental landscape, patch, array, and plot).

	Hypothesis	**Experimental Landscape**	**Patch**	**Array**	**Plot**
(H_1)	*Lespedeza cuneata* abundance is more negatively affected by fires during the growing season than during the dormant season	Reject	Reject	Reject	Reject
(H_2)	Integrating herbicide into pyric herbivory management regimes more effectively reduces *L. cuneata* abundance than management with pyric herbivory alone	Reject	Reject	Mixed	Fail to Reject
(H_3)	Landscapes burned during the growing season have higher plant diversity compared to those burned during the dormant season	Reject	Reject	Reject	Reject
(H_4)	Landscapes with pyric herbivory and herbicide have higher plant diversity compared to landscapes left unsprayed	Reject	Reject	Mixed	Reject
(H_5)	*L. cuneata* abundance is negatively related to biodiversity	Reject	Mixed	Fail to Reject	Fail to Reject
(H_6)	*L. cuneata* abundance is negatively related to other plant functional group abundances	Reject	Mixed	Mixed	Mixed

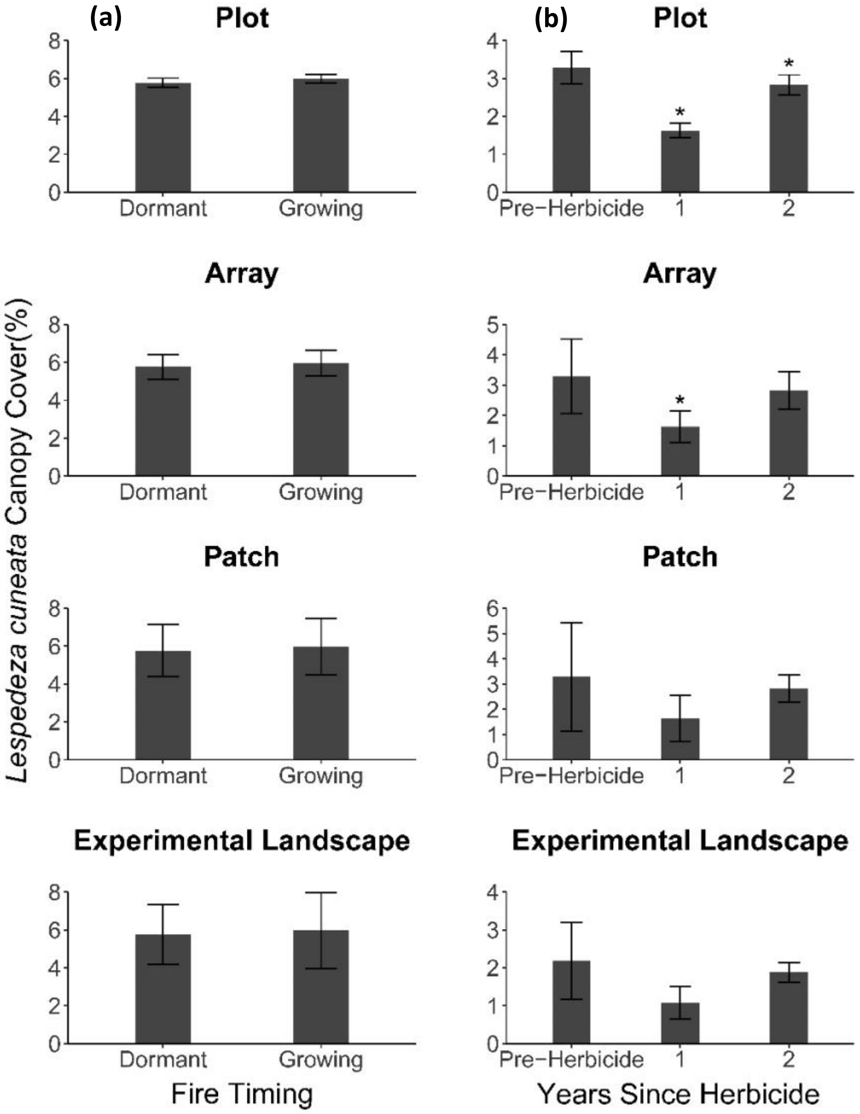

Figure 4.1: *Lespedeza cuneata* canopy cover (%) response to (a) fire during the dormant or growing season, and (b) herbicide treatment through time. Fire timing and herbicide figures only represent data from experimental landscapes that only received the corresponding treatment (e.g., fire timing (a) figures are only from landscapes that did not receive an herbicide application). Error bars represent standard error around the mean. Significant differences determined using linear models, where dormant season fire timing (a) and pre-herbicide (b) were used as the intercept. Significance is denoted by an asterisk (*), representing cases when $p < 0.05$ (i.e., $\alpha = 0.05$).

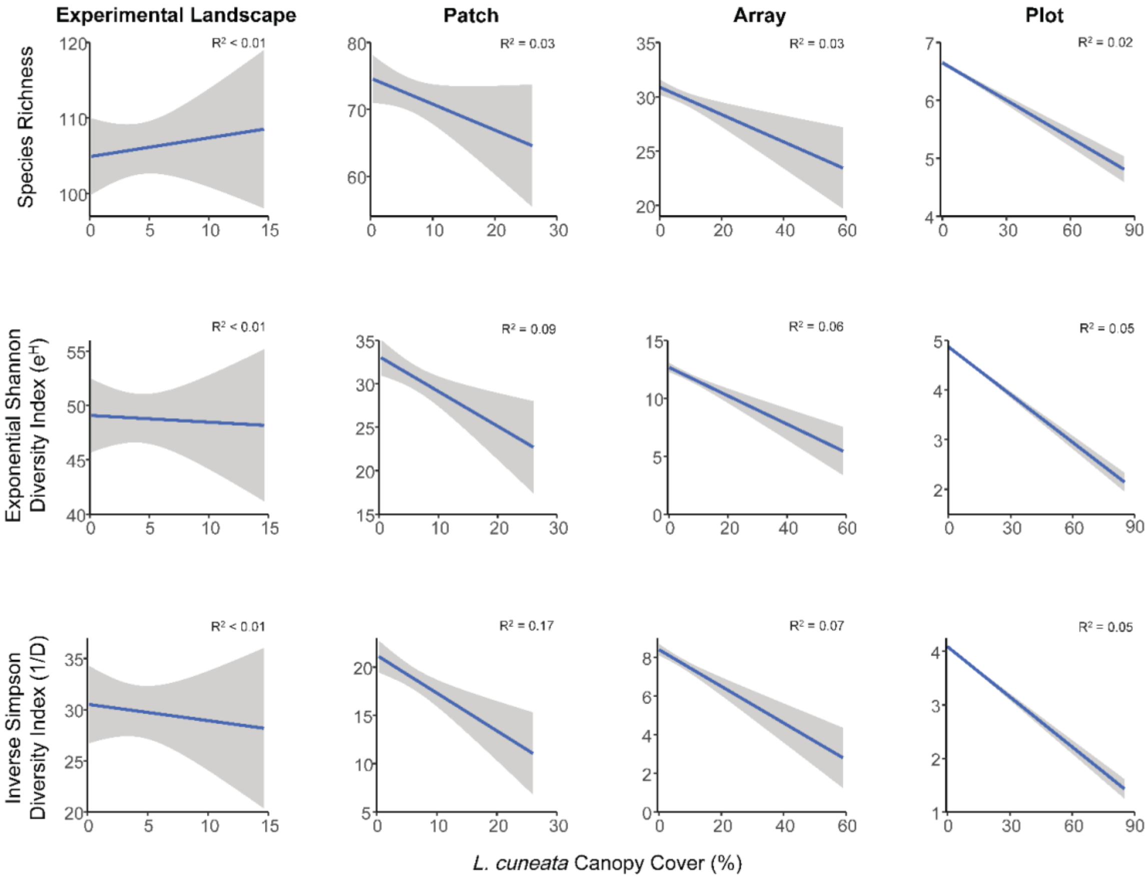

Figure 4.2: Species Richness, Exponential Shannon Diversity Index (e^H), and Inverse Simpson Diversity Index (1/D) responses to *Lespedeza cuneata* canopy cover (%) at the experimental landscape, patch, array, and plot scales. Lines were fit using a linear mixed-modelling approach to account for repeated sampling at each scale. Models at the experimental landscape scale used unique landscape IDs as the random intercept effect, and a unique burn patch ID was used as the random intercept effect in our models at all other scales analyzed in this study. We report the variance explained by each model as the marginal R^2; i.e., the variance explained by the fixed effects in each model. Models represent data collected each July 1-30 from 2019-2021. Note: y-axes do not all start at zero. Fitted line included to illustrate directionality, not to indicate significance. Shaded area represents a 95% confidence interval around the estimate.

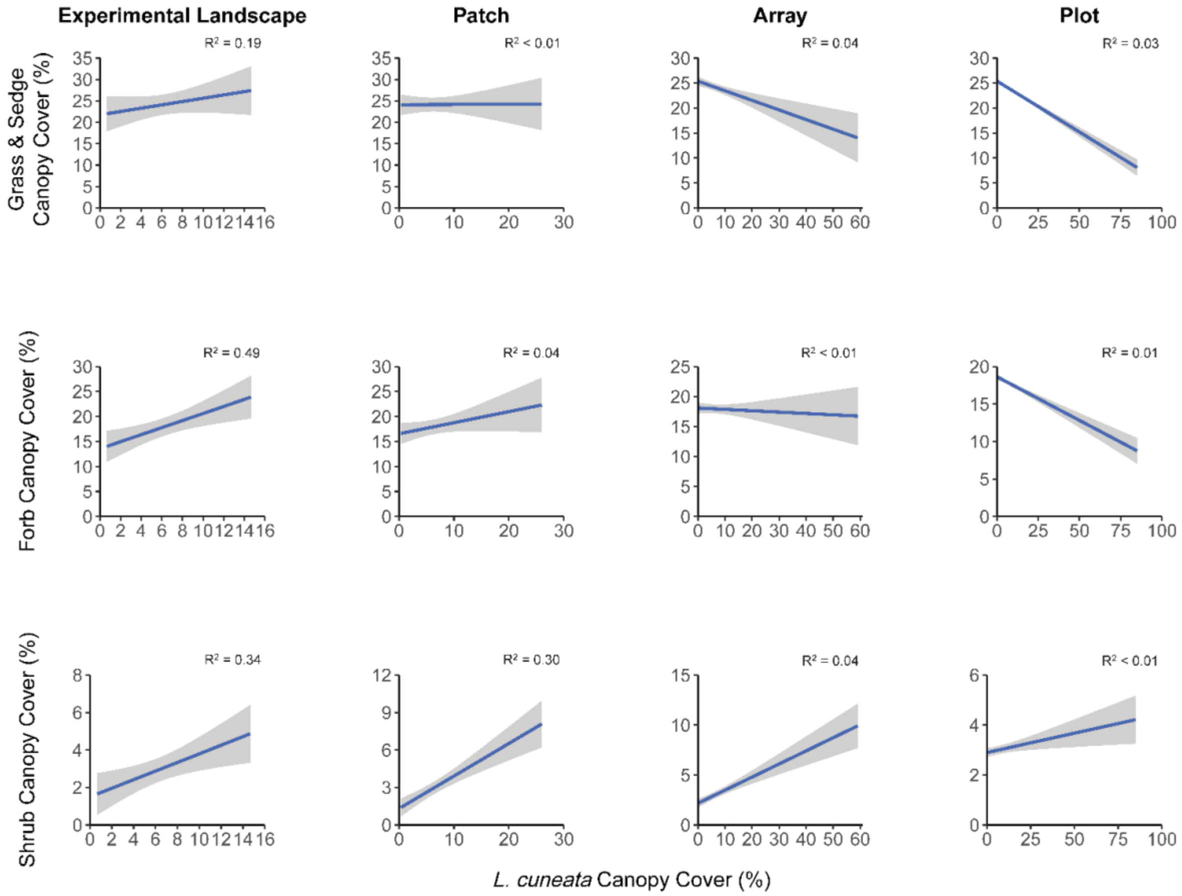

Figure 4.3: Grass & Sedge, Forb, and Shrub abundance (% canopy cover) responses to *Lespedeza cuneata* abundance (canopy cover %) at the experimental landscape, patch, array, and plot scales. Functional group abundances (e.g., forb canopy cover) do not include *L. cuneata*. Lines were fit using a linear mixed-modelling approach to account for repeated sampling at each scale. Models at the experimental landscape scale used unique landscape IDs as the random slope effect, and a unique burn patch ID was used as the random slope effect in our models at all other scales analyzed in this study. We report the variance explained by each model as the marginal R^2; i.e., the variance explained by the fixed effects in each model. Models represent data collected each July 1-30 from 2019-2021. Fitted line included to illustrate directionality, not to indicate significance. Shaded area represents a 95% confidence interval around the estimate.

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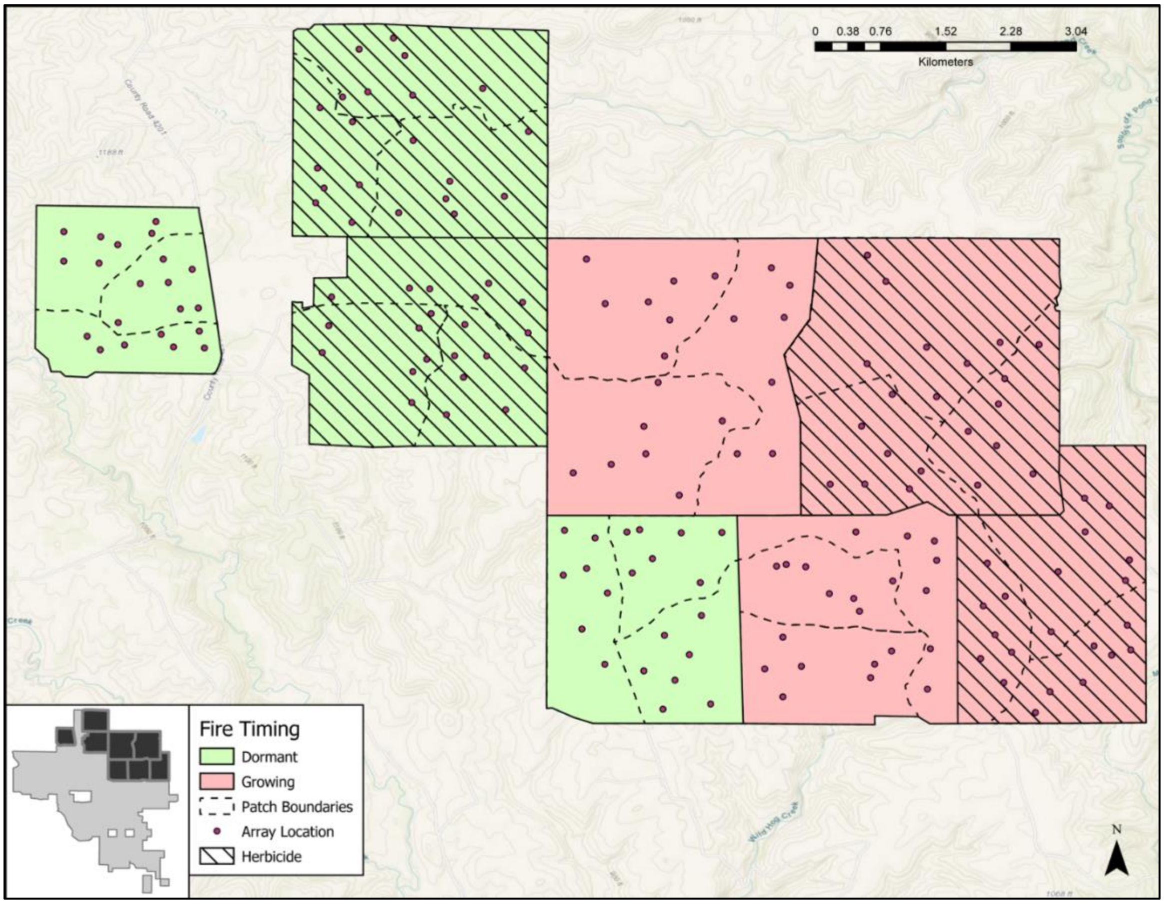
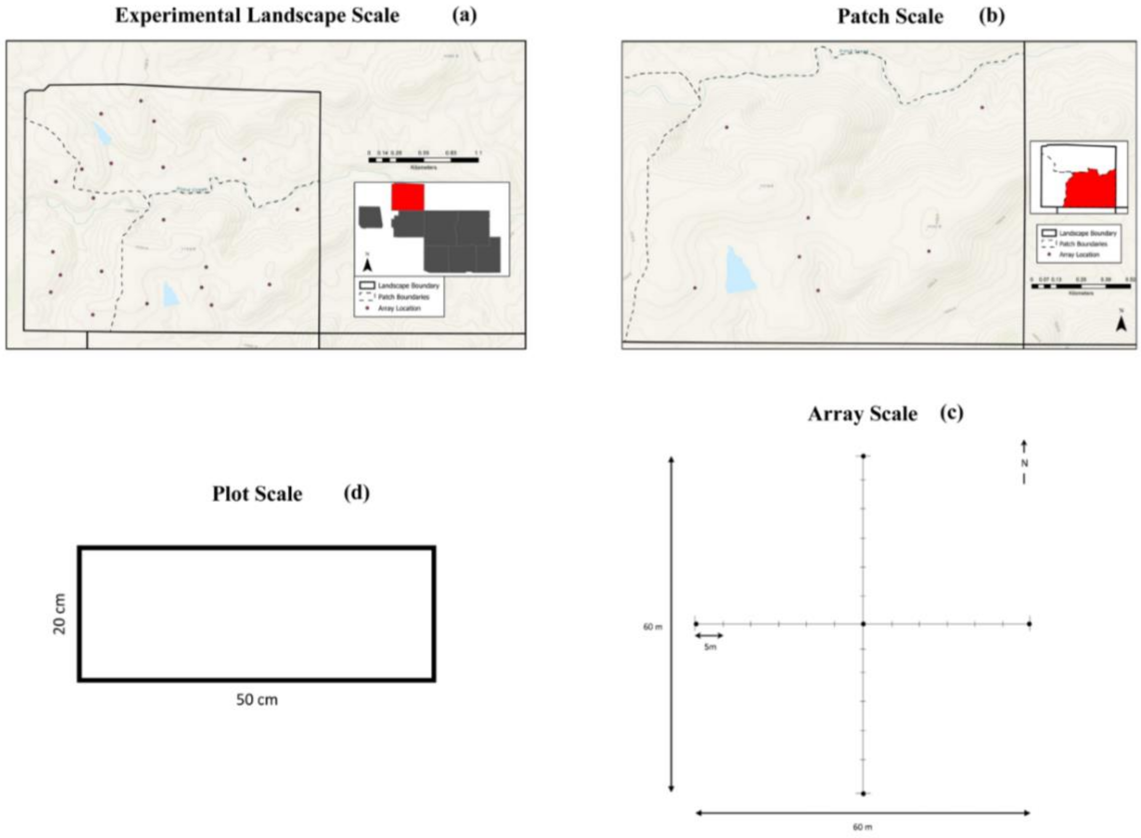
APPENDICES



Appendix A: Map showing the layout of our experimental landscapes (polygons), patches (dashed lines), and array locations (points) across our study area at the Nature Conservancy's Joseph H. Williams Tallgrass Prairie Preserve. The map also shows whether landscapes were burned during the dormant season (i.e., March – April; green polygons) or the growing season (i.e., August – September; red polygons), and whether they were also treated with herbicide (hatched lines).



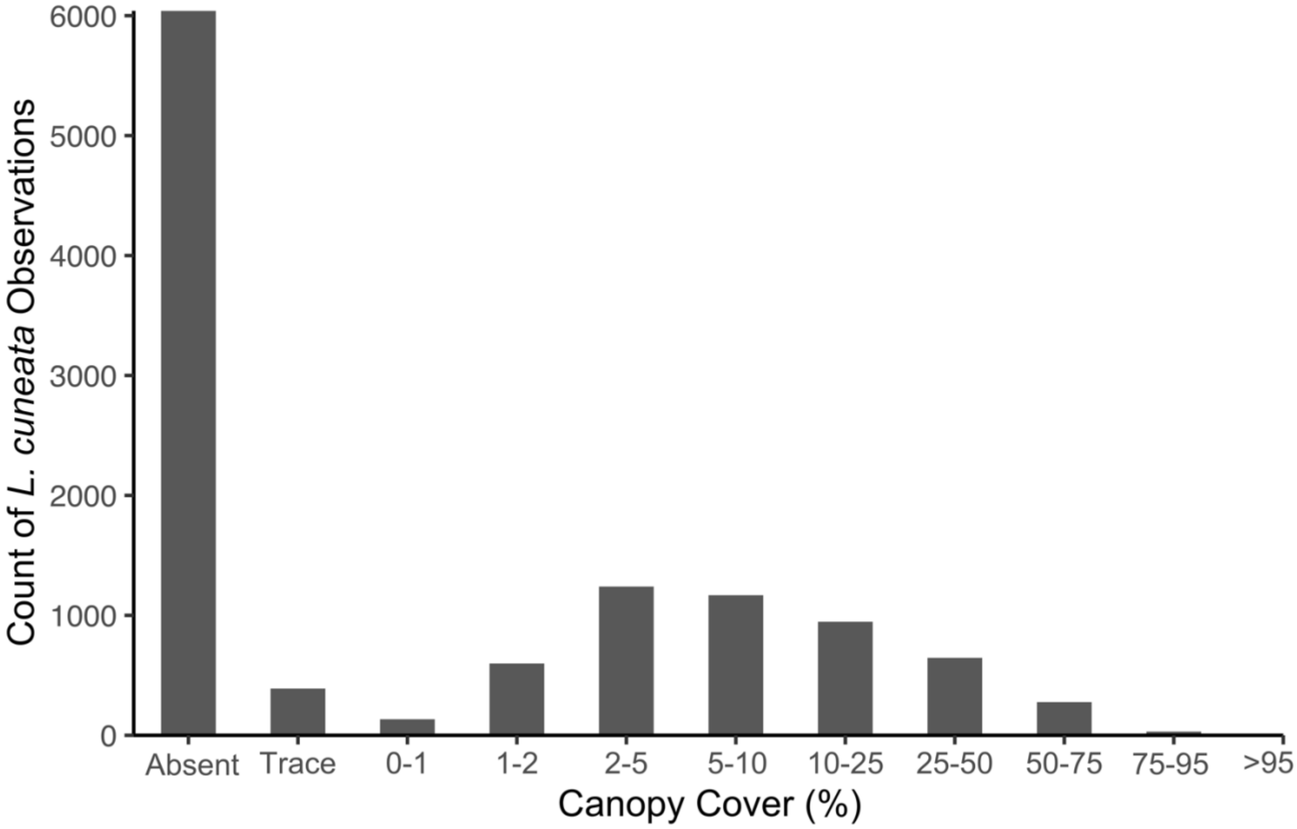
Appendix B: Diagram showing the differences among our experimental landscape (a), patch (b), array (c), and plot (d) scales. Dashed Lines in the experimental landscape (a) and patch (b) scale figures represent patch boundaries, points in those figures represent array locations. Dashed lines in the array scale (c) figure represent plot locations, spaced every 5-meters along each 60-meter transect.

Appendix C: Diversity response to herbicide application through time at the plot, array, patch, and experimental landscape scales. Models fit using linear mixed-models. Landscape ID was used as the random intercept term in models at the experimental landscape scale. Burn patch ID was used as the random intercept term for models at all other scales. Models only included data from experimental landscapes that received an herbicide treatment, and did not include those that were unsprayed. Models represent data collected each July 1-30 from 2019-2021. All data are from landscapes managed with pyric herbivory.

Scale	**Diversity Metric**	**Time Since Herbicide**	**Estimate**	**SE**	**t-value**	**p-value**	**Marginal R^2**	**Total Observations**
Plot	Species Richness	Pre-Application (Intercept)	6.61	0.25	26.52	< 0.01*	--	4,032
		1 Year	-1.08	0.09	-11.92	< 0.01*	0.04	
		2 Years	-0.54	0.06	-8.52	< 0.01*	0.04	
	Exponential Shannon	Pre-Application (Intercept)	4.73	0.17	27.45	< 0.01*	--	4,032
		1 Year	-0.55	0.08	-6.54	< 0.01*	0.02	
		2 Years	-0.46	0.06	-7.68	< 0.01*	0.02	
	Inverse Simpson	Pre-Application (Intercept)	4.04	0.14	27.70	< 0.01*	--	4,032
		1 Year	-0.55	0.08	-6.62	< 0.01*	0.03	
		2 Years	-0.56	0.06	-9.54	< 0.01*	0.03	
Array	Species Richness	Pre-Application (Intercept)	30.17	0.85	35.57	< 0.01*	--	168
		1 Year	-4.27	1.16	-3.69	< 0.01*	0.09	
		2 Years	-2.30	0.84	-2.73	0.01*	0.09	
	Exponential Shannon	Pre-Application (Intercept)	10.83	0.41	26.26	< 0.01*	--	168
		1 Year	0.96	0.75	1.28	0.20	0.01	
		2 Years	0.48	0.57	0.84	0.40	0.01	
	Inverse Simpson	Pre-Application (Intercept)	6.91	0.31	22.29	< 0.01*	--	168
		1 Year	1.25	0.57	2.17	0.03*	0.03	
		2 Years	0.52	0.44	1.18	0.24	0.03	
Patch	Species Richness	Pre-Application (Intercept)	71.81	3.06	23.46	< 0.01*	--	24
		1 Year	-12.72	4.92	-2.58	0.02*	0.22	
		2 Years	-8.06	3.65	-2.20	0.04*	0.22	
	Exponential Shannon	Pre-Application (Intercept)	29.62	1.81	16.36	< 0.01*	--	24
		1 Year	-0.94	3.62	-0.26	0.79	0.04	
		2 Years	-2.73	2.86	-0.95	0.35	0.04	
	Inverse Simpson	Pre-Application (Intercept)	18.08	1.44	12.55	< 0.01*	--	24
		1 Year	-0.29	2.88	-0.10	0.92	0.04	
		2 Years	-2.09	2.28	-0.92	0.37	0.04	
Experimental Landscape	Species Richness	Pre-Application (Intercept)	109.25	3.84	28.45	< 0.01*	--	12
		1 Year	-13.75	4.15	-3.31	0.02*	0.37	
		2 Years	-7.75	4.15	-1.86	0.11	0.37	
	Exponential Shannon	Pre-Application (Intercept)	49.70	3.43	14.50	< 0.01*	--	12
		1 Year	-2.30	3.75	-0.61	0.56	0.05	
		2 Years	-3.44	3.75	-0.92	0.39	0.05	
	Inverse Simpson	Pre-Application (Intercept)	30.59	4.01	7.46	< 0.01*	--	12
		1 Year	-2.07	4.15	-0.50	0.63	0.02	
		2 Years	-2.71	4.15	-0.65	0.54	0.02	

Appendix D: Functional Group Abundance (% Cover) response to *Lespedeza cuneata* abundance (% Cover). Models fit using linear mixed-models. Landscape ID was used as the random intercept term in models at the experimental landscape scale. Burn patch ID was used as the random intercept term for models at all other scales. Functional group abundances do not include *L. cuneata*. Models represent data collected each July 1-30 from 2019-2021. All data are from landscapes managed with pyric herbivory.

Scale	**Functional Group**	**intercept**	**estimate**	**SE**	**t-value**	**p-value**	**Marginal R^2**	**Total Obs.**
Plot	Grasses & Sedges	25.53	-0.22	0.01	-20.01	*< 0.01**	0.03	12,096
	Forbs	18.68	-0.12	0.01	-10.36	*< 0.01**	0.01	
	Shrubs	2.99	-0.01	0.01	-0.66	0.51	< 0.01	
Array	Grasses & Sedges	25.55	-0.22	0.05	-4.47	*< 0.01**	0.04	504
	Forbs	18.03	-0.01	0.05	-0.25	0.80	< 0.01	
	Shrubs	2.39	0.09	0.02	5.30	*< 0.01**	0.04	
Patch	Grasses & Sedges	24.08	0.01	0.15	0.05	0.96	< 0.01	72
	Forbs	16.53	0.22	0.13	1.66	0.10	0.04	
	Shrubs	1.36	0.25	0.04	5.73	*< 0.01**	0.30	
Experimental Landscape	Grasses & Sedges	13.99	0.83	0.31	2.67	*0.01**	0.19	24
	Forbs	7.47	1.34	0.26	5.14	*< 0.01**	0.49	
	Shrubs	0.99	0.30	0.07	4.06	*< 0.01**	0.34	



Appendix E: Total *Lespedeza cuneata* observations by canopy cover (%) at the plot scale (0.1 m^2; n = 12,096 individual samples), across our study area from 2019-2021.

VITA

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